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Systematics and biogeography of *Cyrtandra*: a mega diverse genus in the Malesian hotspot.

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2020

Declaration

I declare that the thesis has been composed by myself and that the work has not been submitted for any other degree or professional qualification. I confirm that the work submitted is my own, except where work which has formed part of jointly-authored publications has been included. My contribution and those of the other authors to this work have been explicitly indicated (Appendix 1). I confirm that appropriate credit has been given within this thesis where reference has been made to the work of others.

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9 April 2020

Abstract

Tropical rain forests are the most biologically diverse of terrestrial biomes. A few species-rich genera contribute disproportionately to this diversity and yet have often been neglected taxonomically because their sheer size makes them so challenging. Understanding the causes and mechanisms of these lineage diversifications is, however, central to understanding the evolution of plant diversity and for effectively planning its conservation. To realise the potential of these large genera, time-calibrated, phylogenetic studies are required to place the species in their evolutionary and biogeographic context, effectively plan future taxonomic work and to investigate the patterns and processes of their diversification.

Cyrtandra is the largest genus in the Gesneriaceae with over 800 species of herbs, shrubs and occasionally trees, and is one of the fifty largest plant genera in the world. It is found from the Nicobar Islands in the Indian Ocean, throughout Malesia, in Taiwan and the southern Japanese islands, in northern Australia and east across Polynesia to Hawaii. It is found in forest, from sea level to 3000m. Taxonomic work is required throughout the distribution of *Cyrtandra* but primarily in its centres of diversity in Southeast Asia, on islands such as Sulawesi and Borneo. There is no functional infrageneric classification in the genus greatly increasing the difficulty of working with the group and hampering the planning of future taxonomic work.

This study includes a taxonomic revision of *Cyrtandra* on the Indonesian island of Sulawesi which has resulted in the recognition of 40 species. Of these, five species are highlighted as new in this thesis: *Cyrtandra longistamina* H.J.Atkins & Karton. ined., *Cyrtandra balgooyi* H.J.Atkins & Karton. ined. *Cyrtandra flavomaculata* H.J.Atkins & Karton. ined., *Cyrtandra parvicalyx* H.J.Atkins & Karton. ined. and *Cyrtandra sopuensis* H.J.Atkins & Karton. ined. Eleven species are lectotypified and three names are placed in to synonymy. Provisional conservation assessments show that two of these species are Critically Endanagered, one is Endangered, thirteen are Vulnerable, one is Near Threatened and 22 are of Least concern.

Generation of a well-sampled phylogeny of *Cyrtandra* across Southeast Asia and the Pacific and optimisation of eight macromorphological characters, as part of the current study, has allowed the development of a strategy for tackling this large genus taxonomically in the future in the absence of a functional infrageneric system. The poor diagnosability of the six major clades, the homoplasy of the macromorphological characters, combined with some degree of floristic exchange between

islands, showed that a single approach, either based on geography, morphology or molecular data, would not be satisfactory for *Cyrtandra* and, similar to other large genera, an integrative method would be most successful. I assessed Clark et al. (2013)'s concept of a phylogenetically informed revision of a geographic area on the *Cyrtandra* of Sulawesi and Borneo and found it to be a promising approach. I now have a key to fourteen lineages on Borneo that can form the basis for taxonomic research on the 200 plus species on that island in the future.

Molecular dating, ancestral range estimation and biogeographic stochastic mapping included here have allowed the examination of the geo-temporal patterns and evolution of southeast Asian *Cyrtandra* and to show that the great diversity of *Cyrtandra* seen in the Malesian region results from a recent radiation, with most speciation taking place in the last five million years. Borneo was recovered as the most likely ancestral range of the genus, with the current distribution of species resulting from a west to east migration across Malesia that corresponds with island emergence and mountain building. High levels of floristic exchange between the islands on the Sunda shelf and an important role for the Philippines as a stepping stone to Wallacea and New Guinea are uncovered. These patterns underlie much of the plant diversity in the region and form an emerging paradigm in Southeast Asian plant biogeography.

Novel observations on speciation dynamics for southeast Asian *Cyrtandra* made here include (i) the absence of hybridisation*,* possiby due to the role of pre-zygotic barriers associated with high levels of floral divergence in sympatric populations in southeast Asia; (ii) a remarkably stable genome with no variation in chromosome numbers recorded across its distribution, including the Pacific. These two observations are notable as they are in contrast to other large genera such as *Begonia, Inga* and *Solanum* where hybridisation and ploidy changes are common.

The dense phylogenetic sampling for interspecific and intraspecific diversity, combined with new trait and geographical datasets have provided much insight into the origin of the diversity of *Cyrtandra.* Future work can focus on the taxonomy of *Cyrtandra* on the large islands of Borneo and New Guinea and on the genomic architecture of species differences.

Lay Summary

There are more species of plants in rain forests than anywhere else in the world. Some groups of plants contribute disproportionately to this diversity, containing exceptionally high numbers of species. These groups have often been neglected by plant scientists because the large number of species makes them difficult to study. However, understanding how so many species have arisen, and how they are maintained in these groups is key to understanding rain forest diversity and planning its effective conservation.

The first step in this type of research is to accurately document the plants in the group by carrying out a taxonomic revision. This involves understanding the variation within each species, describing in detail what they look like and where they grow and giving each species a scientific name. This can then be followed by sequencing of their DNA to build an evolutionary tree which tells us how the species are related to each other. This tree can also be dated using information from fossils so that we can find out whether the high number of species have evolved recently or over a long period of time.

This study has focused on a genus of rain forest plants called *Cyrtandra.* They are understorey plants found on the forest floor or as epiphytes. The group is found throughout Southeast Asia and the islands of the Pacific. There are about 800 species making it one of the top 50 largest plant genera in the world. Taxonomic research is required throughout its distribution, especially on the islands of Southeast Asia where the species numbers are highest. One such island is Sulawesi. Fieldwork and taxonomic research has revealed that there are 40 species on the island and provisional conservation assessments show that sixteen of these are threatened to some degree.

The dated evolutionary tree has shown us that there is no evidence in this data set of either hybridisation between species or changes in chromosome number which can be important processes in generating new species in other species-rich groups. It also revealed that *Cyrtandra* originated on the island of Borneo c. 13 million years ago and then migrated from west to east across the region in to the Pacific. Most of the species are less than 5 million years old meaning that the high levels of diversity that we now see are largely the result of recent speciation.

Acknowledgements

Special thanks to my excellent supervisors Mark Hughes, Catherine Kidner and Toby Pennington for their expertise, support and enthusiasm throughout the PhD.

The Royal Botanic Garden Edinburgh (RBGE) is a fantastic place to work and there are many people there who I would like to thank. Thank you firstly to David Harris, Toby Pennington and Pete Hollingsworth for suggesting that I start a PhD in the first place and for facilitating me to do it part time alongside my role at RBGE.

I would also like to thank Michael Moeller for his generosity with time and Gesneriaceae expertise; Kanae Nishii for her meticulous skills in the lab and her significant contribution to this thesis in terms of DNA extractions and sequence data; Michelle Hart, Laura Forrest and Ruth Hollands for their endless patience and support in the lab; Martin Pullan for the Padme database which is the backbone of the taxonomic revision chapter; Sadie Barber, Nathan Kelson and Stephen Willis for their expert care of the *Cyrtandra* living collections, a vital resource for this study; the herbarium staff for their continuous support providing working space, requesting loans and imaging and mounting specimens; and the library staff, particularly Graham Hardy, for tracking down some obscure references for me.

The Tropical Room at the Gardens has been a source of great conversations, technical support and laughter and I would like to thank the many occupants who I have shared the room with over the past six years: Peter Moonlight, Axel Dalberg Poulsen, Barbara Mackinder, Tiina Sarkinen, Greg Kenicer, Zoe Goodwin, Rebecca Hilgenhoff and Edeline Gagnon. Outside of the Tropical Room, there are too many people to name but I would particularly like to thank Peter Wilkie, Rachael Brewer, Lesley Scott and Jacqui Pestell for their friendship and support through the long haul of this PhD. A lot of fellow PhD students have also helped me along the way and I would particularly like to thank Subhani Ranasinghe and Flavia Pezzini.

The beautiful pen and ink illustrations included in Chapter Two were done by Claire Banks and Christina Oliver; artists of exceptional skill who have taught me so much and allowed me to improve my descriptions through their incredible attention to detail and skilled observations.

The high quality photographs in the colour plates in Chapters Two and Three were taken by Sadie Barber, Wisnu Ardi, Abdulrokhman Kartonegoro, Randi Agusti and Deden Girmansyah and I thank them for allowing me to include them here.

Cyrtandra research has always been extremely collaborative and positive. I hugely value my *Cyrtandra* colleagues: Gemma Bramley, Abdulrokhamn Kartonegoro, Melissa Johnson and Jay Edneil Olivar. Thank you for our useful discussions and the many additional samples and determinations that you have provided for inclusion in this study. I hope that we will continue to work together for many years to come. There is so much to do!

In Indonesia, I would like to thank RISTEK for granting permission for fieldwork in Sulawesi and the staff of the Kebun Raya, Bogor and Herbarium Bogoriense for their time and expertise in facilitating it. I would particularly like to thank our main collaborators and friends: Abdulrokhman Kartonegoro, Marlina Ardiyani, Deden Girmansyah, Wisnu Ardi and Prima Hutabarat. In Sulawesi, we were helped enormously by Julianus Kinho from the Manado Institute of Forestry who came in to the field with us and organised the logistics. Fieldwork in Indonesia was made much easier, and more fun, thanks to the RBGE staff who were with me: thanks to Mark Hughes, Peter Wilkie, Helen Yeats and, especially, Sadie Barber, who led the trip to Sulawesi and was meticulous in her attention to detail, as well as being great company.

In addition to my supervisors, a number of people have read through drafts of the thesis along the way and made invaluable contributions and I would like to thank Sandy Atkins, Gemma Bramley, Mark Coode, David Middleton and Peter Wilkie for their time and expertise.

A number of sources of additional funding have been critical for allowing me to deliver this thesis and include: the Sibbald Trust for funding extra sequencing and for supporting a visit to RBGE by Abdulrokhamn Kartonegoro to allow us to work together on the taxonomic revision; the Gesneriad Society Elwin McDonald fund for additional sequencing; the Davis Fund for fieldwork in Sulawesi and the Singapore Fellowship for a herbarium visit to Singapore Botanic Garden.

On a personal note, I would like to thank my family: Grace and Tom were at primary school when I started and are now both towering above me and leading their own busy lives. They have tolerated me being away for periods of time in Indonesia, for conferences and herbarium visits and occasionally missing out on important events. And a special thank you to David who has supported me every step of the way and given me the confidence to keep going.

Preface

The research for this thesis has been carried out part time whilst I have also been working as a member of staff at the Royal Botanic Garden Edinburgh. Due to the collaborative and international nature of botanical research, particularly relevant when working on a large taxonomic group like *Cyrtandra,* I have been fortunate enough to develop strong links with many researchers in institutions around the world. We have endeavoured to publish as much of our research as possible as it has become completed and, whilst the main taxonomic emphasis of this project has been producing a taxonomic revision of *Cyrtandra* in Sulawesi and assessing the infrageneric structure of the genus in southeast Asia, a number of other smaller taxonomic questions, including the description of new species and resolving species limits in widespread species, such as *Cyrtandra cumingii,* have been resolved as part of this ongoing work. These have been published in collaboration with other taxonomists and are included here in the Appendix (Kartonegoro et al., 2018; Atkins et al., 2019; Nishii et al., 2019). My contribution to each of these papers is detailed in the declaration. The overall structure of the thesis also reflects the requirement for publication and each chapter is presented in the form of a paper, formatted in the relevant journal style. Chapter Four on the biogeography of the genus has already been published and the final paper is included in the Appendix. The version of the paper as it was first submitted to *Frontiers in Biogeography* is included as Chapter Four.

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Chapter One: Introduction and Aims

Tropical rain forests are the most biologically diverse of terrestrial biomes (Richardson et al., 2001; Losos & Leigh, 2004; Harrison, 2005; Dick & Kress, 2009). A few species-rich genera, such as *Piper, Dipterocarpus, Euphorbia, Ficus, Begonia, Macaranga, Solanum* and *Inga* contribute disproportionately to this diversity (Richardson et al., 2001; Frodin, 2004; Losos & Leigh, 2004; Harrison, 2005; Thomas et al., 2012; van Welzen et al., 2009) and yet these large genera have often been neglected taxonomically because their sheer size makes them challenging (Bramley, 2003; Frodin, 2004; van Welzen et al., 2009; Moonlight et al., 2018; Nic Lughada et al., 2019), often rendering them 'taxonomic black holes' (Moonlight et al., 2018) where species boundaries are uncertain and many new species await description. Understanding the causes and mechanisms of these lineage diversifications is, however, central to understanding the evolution of plant diversity (Richardson et al., 2001; Hughes et al., 2015) and for effectively planning their conservation (Winter et al., 2013; Nic Lughada et al., 2019). To realise the potential of these large genera, time-calibrated, phylogenetic studies are required to place the species in their evolutionary and biogeographic context, effectively plan future taxonomic work (Knapp, 2008; Dick & Kress, 2009; Nic Lughada et al., 2019) and to investigate the patterns and processes of their diversification (Linder, 2008; Hughes et al., 2015).

Cyrtandra is the largest genus in the Gesneriaceae with over 800 species of herbs, shrubs and occasionally trees (Burtt, 2001; Atkins et al., 2013) and is one of the fifty largest angiosperm plant genera in the world (Frodin, 2004). It is found from the Nicobar Islands in the Indian Ocean, throughout Malesia, in Taiwan and the southern Japanese islands, in northern Australia and east across Polynesia to Hawaii. It is recorded on the Asian continent as far north as central Thailand (Fig. 1.1). Its centres of diversity in Malesia are New Guinea and Borneo (each with over 150 species) and the Philippines (with over 80 species) and approximately 175 species are also distributed across the Pacific Basin, with every major archipelago hosting numerous endemic species (Atkins et al., 2013; Johnson et al., 2017). It is found predominantly in the rain forest, from sea level to 3000m (Burtt 2001; Atkins et al., 2013).

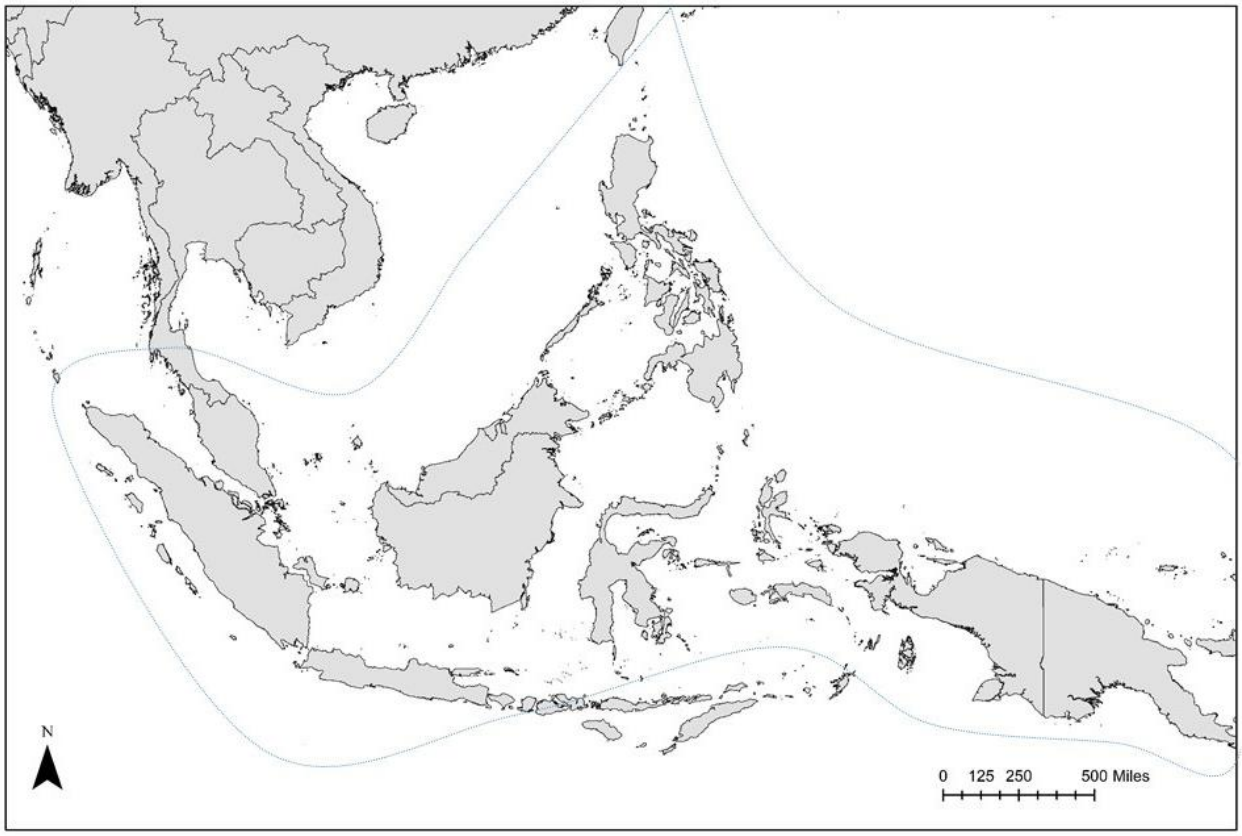
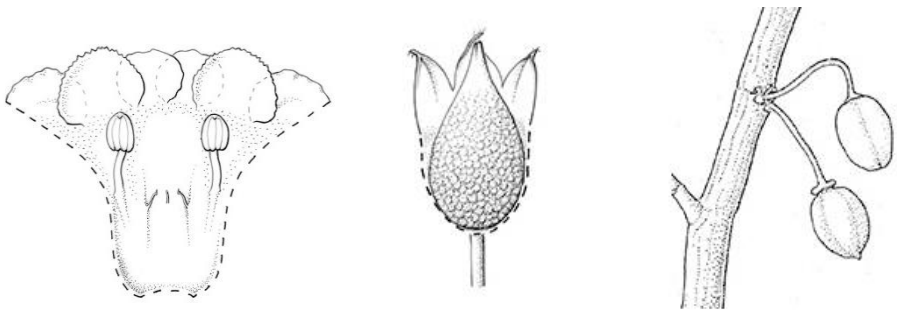


Fig 1.1 Distribution of *Cyrtandra* in Southeast Asia

Cyrtandra is defined morphologically within Gesneriaceae by its unique combination of two fertile stamens and indehiscent fruits (Burtt, 2001; Atkins et al., 2013). Fig. 1.2. In both recent family-wide molecular phylogenetic studies (Weber et al., 2013; Luna et al., 2019) and *Cyrtandra*-focused research (Bramley et al., 2004; Clark et al., 2009; Johnson et al., 2017; Atkins et al., 2020) the genus is resolved as monophyletic with high branch support.



a b

Fig. 1.2 Diagnostic characters for *Cyrtandra* a. two fertile stamens and b. indehiscent fruits

Cyrtandra was first described in 1776 (Forster & Forster, 1776) based on two species from the Pacific. The only taxonomist to attempt a classification system for *Cyrtandra* across its distribution is Clarke (Clarke, 1883). Working with far fewer specimens than are now available, he recognised 164 species of *Cyrtandra,* which he divided into two subgenera and thirteen sections. Subsequently, and due to shortcomings in Clarke's system, two additonal sectional classifications were developed based on geographic subsets: one for Hawaiian *Cyrtandra* (Hillebrand, 1883) and one for the genus in New Guinea (Schlechter, 1923). In addition, many new species have been described from across the distribution of the genus, notably in Southeast Asia from Borneo (eg Burtt, 1978; 1990; 1992; 1999; Hilliard & Burtt, 2004; 2005; 2006) and the Philippines (eg Kraenzlin, 1906; 1913; 1927; Elmer, 1910; 1915; Merrill, 1907; 1920) and five new sections to accommodate some of the diversity in the Philippines and Borneo (Kraenzlin, 1906; 1913; 1927; Hilliard & Burtt, 2003). Molecular phylogenetic work has primarily focused on the biogeography of the genus (Atkins et al., 2001; Bramley et al., 2004a; Cronk et al., 2005; Clark et al., 2008; 2009; Johnson et al., 2017; 2019) with some taxonomy and classification (Bramley, 2003; Clark et al., 2013). A table detailing the history of research on the genus in Southeast Asia is given in Table 1.1. This includes the papers which are part of the Appendix of this thesis. One of the papers (Atkins et al., 2020) is a published version of Chapter Four; the remaining three (Kartonegoro et al., 2018; Atkins et al., 2019; Nishii et al., 2019) have resulted from collaborative efforts to provide names for as many of the samples included in the published phylogeny (Atkins et al., 2020) as possible.

Basic taxonomic work is still required throughout the distribution of *Cyrtandra* but primarily in its centres of diversity in Southeast Asia, on islands such as Sulawesi (Burtt, 2001; Atkins et al., 2013). The Indonesian island of Sulawesi lies in the heart of Southeast Asia, immediately to the east of Wallace's Line. It is at the centre of one of the most geologically complex and biogeographically interesting areas in the world (Hall, 2002; 2012; Richardson et al., 2012) and yet the flora of the island is remarkably poorly known and under-collected (Frodin, 2001; Kessler et al., 2002; Middleton et al., 2019). Knowledge of the affinities of the flora of Sulawesi is crucial to an understanding of the biogeography of the Southeast Asian region (van Welzen et al., 2011).

Its high diversity, large number of endemic species, and wide distribution make *Cyrtandra* an ideal genus for examining biogeographic patterns (Atkins et al. 2001, Cronk et al. 2005, Clark et al. 2009, Johnson et al. 2017) and investigating the processes which underlie current patterns of biodiversity (Bramley et al. 2004, Johnson et al. 2015, 2019). There is, however, no effective infrageneric classification for this genus (Burtt, 2001; Bramley, 2003), greatly increasing the difficulty of working with this group and hampering the planning of future taxonomic work (Burtt, 2001; Bramley, 2003; Atkins et al., 2013).

The overall aim of this thesis is to document and understand the evolution of the diversity of *Cyrtandra,* a major lineage diversification in southeast Asia. Fundamental to this is an informed understanding of what species are present and the establishment of a taxonomic framework, based on phylogenetic principles, in which to place those species. Secondarily, we will contribute towards our understanding of the diversification by considering when and where it occurred (Linder, 2008) and provide some preliminary insights in to why and how (Hughes et al., 2015).

Objectives:

1. To document the diversity that is present one of the key islands at the centre of diversity of the genus by producing a taxonomic revision of the *Cyrtandra* flora of Sulawesi (Chapter Two)

2. To produce a phylogeny of the genus across its distribution, with an emphasis on the Malesian region, through the sequencing of four chloroplast and one nuclear gene regions.

3. To use the resultant phylogeny to:

    a. Assess the utility of the current infrageneric system for the genus, test for morphological homoplasy and identify candidate characters to build a future classification system. (Chapter Three)
    b. Evaluate the geo-temporal patterns and evolution of the clade in the Malesian region by estimating divergence times, ancestral range and dispersal patterns. (Chapter Four)

Table 1.1. Summary of research in Southeast Asian *Cyrtandra.* Authors are listed chronologically by first publication date. Papers included in the Appendix of this thesis are in bold and asterisked.

Author	Year(s)	Geographic area	Research focus	New Sections/ Subgenera	New species described	Selected Publications
Jack, W.	1823	Sumatra, Java	Taxonomic		12 species	Jack, 1823
Blume, C.L.	1826	Sumatra, Java, Sulawesi	Taxonomic		14 species	Blume, 1826
De Vriese,	1856	Java, Sulawesi	Taxonomic		12 species	De Vriese, 1856
Clarke, C.B.	1883	Full distribution	Taxonomic; infrageneric	2 subgenera, 13 sections	90 species	Clarke, 1883
Schumann, K.	1888-1905	New Guinea	Taxonomic		16 species	Schumann, 1888; Schumann & Lauterbach, 1905
Ridley, H.N.	1893-1937	Peninsular Malaysia	Taxonomic		19 species	Ridley, 1896; 1905
Kraenzlin, F.	1906-1927	Philippines, Borneo	Taxonomic; infrageneric	4 sections	70 species	Kraenzlin, 1906; 1913; 1927
Merrill, E.D.	1906-1929	Philippines, Borneo	Taxonomic		38 species	Merrill, 1907; 1920
Elmer, A.D.E.	1908-1939	Philippines, Borneo	Taxonomic		36 species	Elmer, 1910; 1915.
Lauterbach, C.A.G.	1908-1912	New Guinea	Taxonomic		16 species	Lauterbach, 1910.
Moore, S.	1914-1929	Sumatra, New Guinea	Taxonomic		15 species	Moore, 1916
Schlechter, R.	1923	New Guinea	Taxonomic; infrageneric	2 subgenera; 14 sections	72 species	Schlechter, 1923
Burtt, B.L. & Hilliard, O.H.	1936-2006	Borneo	Taxonomic; infrageneric	1 section	122 species	Burtt, 1978; 1990; 1992; 1999; Hilliard & Burtt, 2004; 2005; 2006.
Bakhuizen van den Brink, R.C.	1950	Java	Taxonomic		4 species	Bakhuizen, 1950
Cronk, Q.C.B.	2001-2005	Philippines, Pacific	Taxonomic; molecular phylogenetics; biogeography		7 species	Cronk et al., 2005
Atkins, H.J.	2001-ongoing	Philippines, Sulawesi, New Guinea	Taxonomic; molecular phylogenetics; biogeography		26 species	Atkins & Cronk, 2001; Atkins, 2004; **Atkins et al.**, 2001, 2013, **2019*, 2020*.**
Bramley, G.L.C.	2003-ongoing	Sumatra, Peninsular Malaysia, Borneo, New Guinea	Taxonomic; molecular phylogenetics; biogeography		6 species	Bramley, 2005; Bramley et al., 2004a; 2004b.
Kartonegoro, A.	2014- ongoing	Sulawesi	Taxonomic; molecular phylogenetics; biogeography		12 species	Kartonegoro & Potter, 2014; ***Kartonegoro et al., 2018.**
Nishii, K.	2019-ongoing	Japan, Taiwan, Philippines	Taxonomic; molecular phylogenetics; biogeography			***Nishii et al., 2019.**
Olivar, J.	2019-ongoing	Philippines	Taxonomic; molecular phylogenetics; biogeography		3 species	Olivar & Muellner-Riehl, 2019; Olivar et al., in press

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Chapter Two: A taxonomic revision of *Cyrtandra* (Gesneriaceae) in Sulawesi, Indonesia

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Taxonomic evaluation of collections from Sulawesi has resulted in the recognition of 40 species. Of these, five species are described as new here: *Cyrtandra longistamina* H.J.Atkins & Karton., *Cyrtandra balgooyi* H.J.Atkins & Karton.*, Cyrtandra flavomaculata* H.J.Atkins & Karton., *Cyrtandra parvicalyx* H.J.Atkins & Karton. and *Cyrtandra sopuensis* H.J.Atkins & Karton.. Eleven species are lectotypified and four names are placed in synonymy. Provisional conservation assessments suggest that two of these species are Critically Endanagered, one is Endangered, thirteen are Vulnerable, one is Near Threatened and 22 are of Least Concern. Illustrations, distribution maps, and a key to the *Cyrtandra* of Sulawesi are presented.

Keywords: new species, Southeast Asia, Sulawesi, taxonomy

2.1 Introduction

Cyrtandra J.R. & G. Forst. (family *Gesneriaceae* subfamily *Didymocarpoideae* tribe *Trichosporae* subtribe *Didymocarpinae)* is a large genus of c. 800 species of herbs, shrubs, climbers, and rarely, trees (Atkins et al., 2013). It is a predominantly Southeast Asian genus, its distribution corresponding to the 'Malesian type' sensu van Balgooy (1971), and is found from the Nicobar Islands in the Indian Ocean, throughout Malesia, in Taiwan and the southern Japanese islands, in northern Australia and east across Polynesia to Hawaii. It is recorded on the Asian continent only as far north as central Thailand and its centres of diversity in Malesia are New Guinea and Borneo (each with over 150 species) and the Philippines (with over 80 species). Approximately 175 species are also distributed

across the Pacific Basin, with every major archipelago hosting numerous endemic species (Atkins et al., 2013). It is found in forest from sea level to over 3000 m altitude.

Sulawesi is the largest island in the region of Wallacea, one of the most complex biogeographic regions in southeast Asia (Cannon et al., 2007). The flora of the island, however, remains poorly known. It was identified in 2001 (Frodin, 2001) as being one of the top ten places in the world most in need of floristic work and plant specimen collection rates on the island are amongst the lowest in Indonesia (Kessler et al., 2002; Cannon et al., 2007; Middleton et al., 2019). The island lies at the centre of one of the most geologically complex areas in the world (Hall, 2002; 2012) and is itself of composite origin. Its position at the meeting point of floras of diverse origins, its complex geology, including some of the largest mafic outcrops in the world (van der Ent et al., 2013) have resulted in a unique flora with high levels of endemism.

The first *Cyrtandra* species to be published from Sulawesi was *Cyrtandra celebica* Blume (Blume, 1826). Following an expedition to the island by Reinwardt in 1821, de Vriese described five species (de Vriese, 1856) and Koorders (1898) added another five following his extended trip to northern Sulawesi. Other than a recombination by Burtt (Burtt, 1990), no new names for Sulawesi *Cyrtandra* were then published for over 100 years (Mendum & Atkins, 2004). Following fieldwork in Gorontalo, North Sulawesi, Central Sulawesi and South East Sulawesi in the early 2000s, a further 23 species have been described in a number of publications (Atkins, 2004; Bone & Atkins, 2013; Kartonegoro & Potter, 2014; Kartonegoro et al., 2018). Five new species are described here bringing the total for the island to 40.

Despite a significant increase in plant collecting across Sulawesi in the last 25 years, particularly from the undercollected South, West and South East provinces, there remain relatively few collections and seven species of *Cyrtandra* from the island have been described from a single collection. This situation is clearly not ideal but with the real possibility that these taxa may not be collected again for many years, or may be lost as a result of habitat destruction, an effort has been made to account for all of the diversity present. Whenever the distinctiveness of a new species is clear we have described it even if, as in the case of *C. spectabilis* R.Bone & H.J.Atkins*,* characters such as fruits, are lacking.

We present here the first taxonomic synthesis of collections from across the island and provide a key, descriptions, distribution maps and conservation assessments for all known species including five new species.

2.2 Materials and Methods

This is a study based on herbarium specimens and most of the dimensions and descriptions for vegetative and fruit characters given are from dried material. Floral descriptions and measurements are either taken from flowers preserved in Copenhagen solution (70% methylated spirit, 28% distilled water and 2% glycerol) or dried flowers rehydrated by boiling following Bridson & Forman (1999). Specimens were studied from the following herbaria: A, BM, BO, CANB, E, K, KB, L (Herbarium acronyms follow Thiers et al., continuously updated).

The species concept adopted here is a morphological one (McDade, 1995; Coyne & Orr, 2004) based on consistent morphological differences between species. As found in other similar studies, c. 80% of the taxa included here presented few problems in terms of species delimitation (McDade, 1995), it being very straightforward to find and describe at least three consistent morphological differences between species. There were, however, a small number of species, particularly the seven species that currently comprise the *Cyrtandra engleri* group (see further discussion under that species) where it was more challenging. Further information, and more collections, are required to discern whether these difficulties are the result of incipient speciation, hybridisation or other biological processes. For now, an attempt has been made to recognise the variation present in as consistent a way as possible across the island based on morphological discontinuities.

Proposals for IUCN conservation categories were made following the IUCN Red List Categories and Criteria and associated guidelines (IUCN, 2012). When more than two collection localities were known for a species, precise geographical co-ordinates known, or georeferenced place names available, these were used to estimate extent of occurrence (EOO) and area of occupancy (AOO; *sensu* IUCN criterion B1) using a 2 km by 2 km grid cell in GeoCAT (Bachman et al., 2011). Because Sulawesi is underexplored (and *Cyrtandra* species under sampled) these calculations probably underestimate true EOO and AOO values, but we feel that their inclusion helps to emphasise the urgent need for more extensive surveying across the island to assess threats to these species

adequately. A set of maps generated for the provisional conservation assessments using the GeoCAT online assessment tool http://geocat.kew.org/ is included as Appendix 2.1 1.

The list of '*Additional specimens examined*' given after each of the species' descriptions are listed first by Province and then alphabetically by collector. The Provinces are listed from north to south in the order: North Sulawesi, Gorontalo, Central Sulawesi, West Sulawesi, South Sulawesi, South East Sulawesi. Where there is more than one collection by the same collector, these are listed in order of collection date.

Forest types referred to in the '*Habitat and Ecology*' sections after each species description, and in the conservation assessments, follow the categories identified by Cannon et al. (2007) in their study of forest types and conservation priorities in Sulawesi. These comprise 'Lowland': 0—400 m asl; 'Hill': 400—850 m asl; 'Upland': 850—1500 m asl; 'Montane': 1500—2500 m asl and 'Tropalpine': > 2500 m.

Literature abbreviations used in the nomenclatural sections follow Harvard University's Index of Publications (https://kiki.huh.harvard.edu/databases/publication_index.html). The first time that a species name is mentioned in the text, the authorities are given following Brummitt & Powell (1992).

Additional notes on diagnostic characters, taxonomic decision-making and nomenclatural issues are given, when appropriate, after each species.

2.3 Characters and Terminology

Leaves

i. The terminology used to describe leaf shapes follows Hickey (1979).

ii. There is a very strong tendency throughout the Gesneriaceae for the two leaves of a pair to be unequal in size to some degree (anisophylly). All of the different states of anisophylly recognised by Hilliard & Burtt (2002) in their monograph of *Agalmyla* are recorded in Sulawesi *Cyrtandra*. At its most extreme, the reduced leaf is represented by a scale-like structure, only about 10–30 mm long, such as in *C. sopuensis* H.J.Atkins & Karton. Elsewhere anisophylly can occur as only a slight

difference in the size of the two leaves or as a great reduction in one of them to a miniature condition, with an overall length sometimes as short as 10 mm but with a clear differentiation into petiole and lamina, such as in *C. widjajae* Karton. Sometimes, one leaf of a pair is apparently absent and the leaves 'appear alternate' such as in *C. bruteliana* Koord. and *C. gorontaloensis* H.J.Atkins, although there is usually some indication of a vestigial structure (Fig. 2.1).

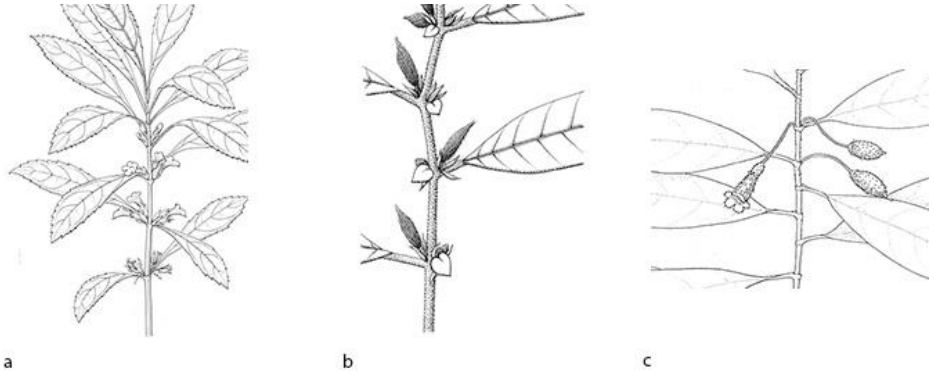


Fig. 2.1 Leaf arrangements: a. Subequal b. Anisophyllous with smaller leaf highly reduced but with a clear differentiation into petiole and lamina c. leaves 'apparently alternate'

iii. For leaf venation, two main characters are described; i. the number of lateral or secondary vein pairs ii the visibility of the tertiary venation (Fig. 2.2). The number of lateral vein pairs varies in Sulawesi *Cyrtandra* from, three to four pairs in small-leaved species like *C. serratifolia* H.J.Atkins, to up to 25 pairs in *C. celebica.* It usually does not vary significantly within a species although the widespread *C. celebica* can have between 9 and 25 pairs. For most species in Sulawesi the tertiary venation is easily visible, and usually reticulate, but there are a few species including *C. purpurea* H.J.Atkins and *C. gambutensis* Karton. & H.J.Atkins where it is very faint. In the majority of specimens the lateral veins curve upwards before terminating at the margin or looping up to join the vein above. There is a single species, *C. gorontaloensis* H.J.Atkins, where the lateral veins run straight out from the midrib and terminate at the margin without looping upwards.

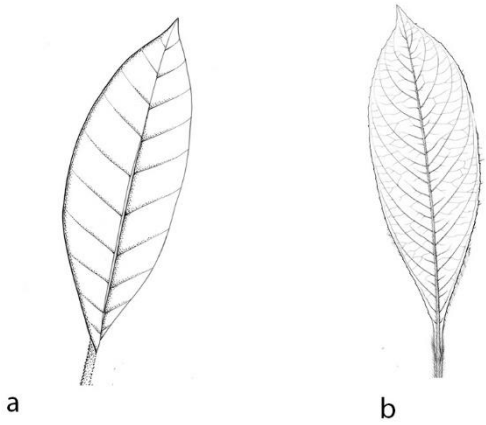


Fig. 2.2 Leaf venation: a. obscure tertiary venation b. visible tertiary venation

Inflorescence position

The majority of species in Sulawesi have axillary inflorescences, either in the axils of current leaves or at the base of the stem below the leaves such as in *C. polyneura* (C.B.Clarke) B.L.Burtt and *C. hendrianii* Karton. & H.J.Atkins. There is one species, *C. celebica,* with cauliflorous inflorescences, and four species which flower on long, trailing stems which originate from the base of the plant (Fig. 2.3). These include *C. hypogaea* Koord*., C. geocarpa* Koord., *C. luteiflora* H.J.Atkins and *C. rantemarioensis* Karton. & R.E.Bone. The term 'inflorescence axis' is used to describe this trailing structure as it is not known whether this is an extended peduncle or modified stem. All four of these trailing species were included in the molecular phylogenetic analysis of southeast Asian *Cyrtandra* (Atkins et al., 2020) and it is clear that this phenomenon has evolved more than once in Sulawesi.

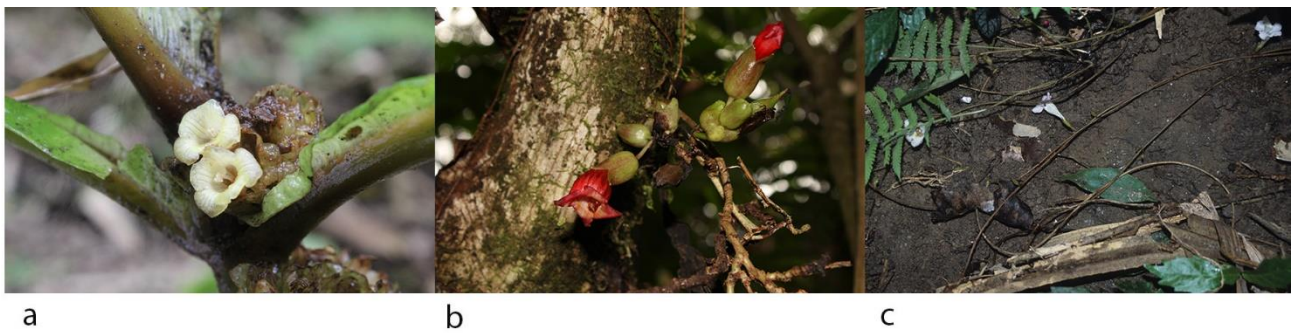


Fig. 2.3 Inflorescence position: a. axillary b. cauliflorous c. on long trailing stems from the base of the plant

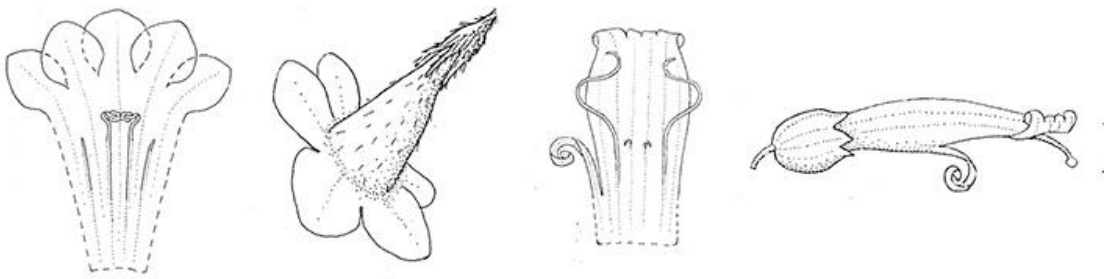
Flowers

Cyrtandra flowers are protandrous; once the anthers have dehisced and the flower moves in to the female phase, the stamens recoil back in to the corolla tube, pulling the anthers apart and the

gynoecium extends. Following Bramley et al. (2003), the descriptions and measurements presented here relate to the mature male and female organs taken from a range of flowers whenever possible.

All corollas are bilabiate to a greater or lesser degree but the corolla limb has two main types: (i) two upper lobes and three lower lobes; and (ii) two upper, two lateral and one lower lobe. The first, and most common group, usually has all lobes 'spreading' i.e. not strongly recurved or extending forwards. This morphology is found in many of the Sulawesi species including *Cyrtandra serratifolia* and *C. engleri* Koord. and is common in the genus as a whole (Fig. 2.4).

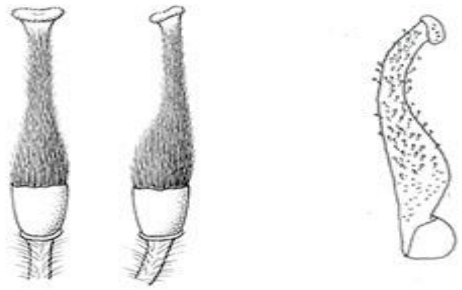
The second group has the lower lobe strongly recurved and the upper and lateral ones either erect, extending forwards or also recurved. There is clearly some variation within this second group in the position of the upper lobes but it is not clear to what extent the recurvation of these lobes varies with age. All of this group have, however, the strongly recurved lower lobe. In some, the lower lobe is much longer than the others and appears like a 'tongue' which is typical of Schlechter's Section *Glossophorae* from New Guinea. In Sulawesi this group includes *Cyrtandra purpurea* H.J.Atkins and *C. longistamina* H.J.Atkins & Karton. (Fig. 2.4).



a b

Fig 2.4 Corolla types: a. two upper lobes and three lower lobes b. two upper, two lateral and one lower lobe.

In this taxonomic account the nectary disc is described as being cupular when it encloses the base of the ovary completely and unilateral where the disc is only present on one side of the ovary (Fig. 2.5). This is usually very clear but there are a few species, such as *C. celebica* and *C. kinhoii* Karton. & H.J.Atkins, where the disc encloses the ovary but is much lower on one side than the other. These are described as cupular, lower on one side. This is consistent with the terminology used by Burtt (1990). The upper margin of the disc is usually glabrous but can sometimes be fringed with eglandular hairs as in *C. gambutensis*.



a b

Fig. 2.5 Disc types: a. cupular b. unilateral

Stigma types

Three stigma types are seen in Sulawesi: bilobed, peltate and capitate (Fig. 2.6). In the species with bilobed stigmas, the lobes are sometimes held upright and sometimes horizontal and spreading. This is recorded in the descriptions although this probably varies as the flower matures as both states are observed in some species, such as *C. kinhoii* and *C. rubribracteata*. For the species with horizontally bilobed, capitate or peltate stigmas, a measurement across the diameter of the exposed stigmatic surface is given. For the species with bilobed stigmas where the lobes are held vertically, often pressed together, a measurement for the length of a single lobe is given.

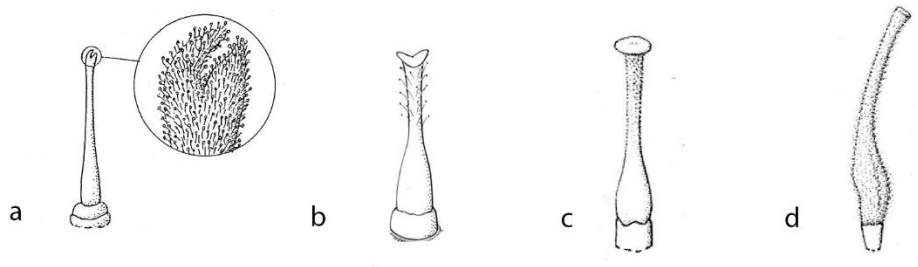


Fig. 2.6 Stigma types: a. bilobed, lobes upright b. bilobed, lobes spreading c. peltate d. capitate.

There are two fertile stamens and usually three staminodes in *Cyrtandra* flowers (Fig. 2.7). For the stamens, filament length and the distance that the the filaments are attached from the base of the corolla are given. The staminodes can either be (a) all approximately the same length, (b) with two

lateral staminodes that are longer and a third, much reduced central staminode or, more rarely, (c) the third staminode does not develop at all (Fig. 2.7).

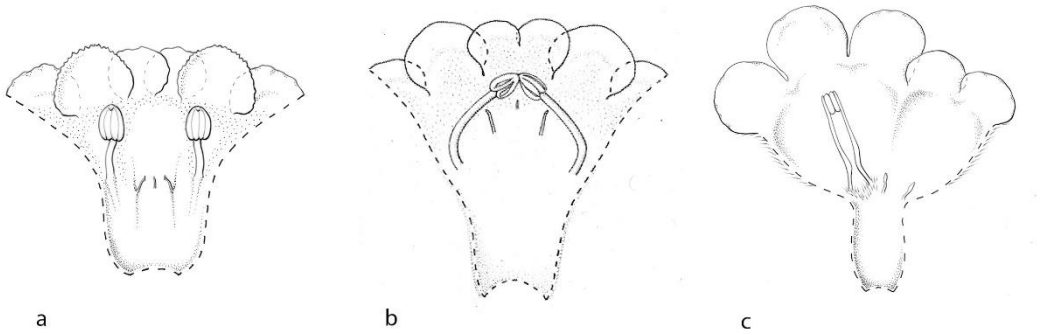


Fig 2.7 Staminodes: a. all staminodes approximately the same length b. central staminode much shorter than the laterals c. two staminodes only.

Fruits

Four main fruit shapes are seen in Sulawesi *Cyrtandra* (Fig. 2.8). The most common fruit types in Sulawesi are ovoid and oblong seen in 37 of the species. There is one species, *C. tenuicarpa,* with very narrow linear fruits, much more commonly seen in Borneo and two species, *C. purpurea* and *C. longistamina* with sub-globose, somewhat fleshy, fruits more often seen in Pacific and New Guinea species. Linear fruits are distinguished from oblong by a ratio of length to width greater than 8 to 1. The persistence of the calyx and base of the style on the mature fruits are also recorded.

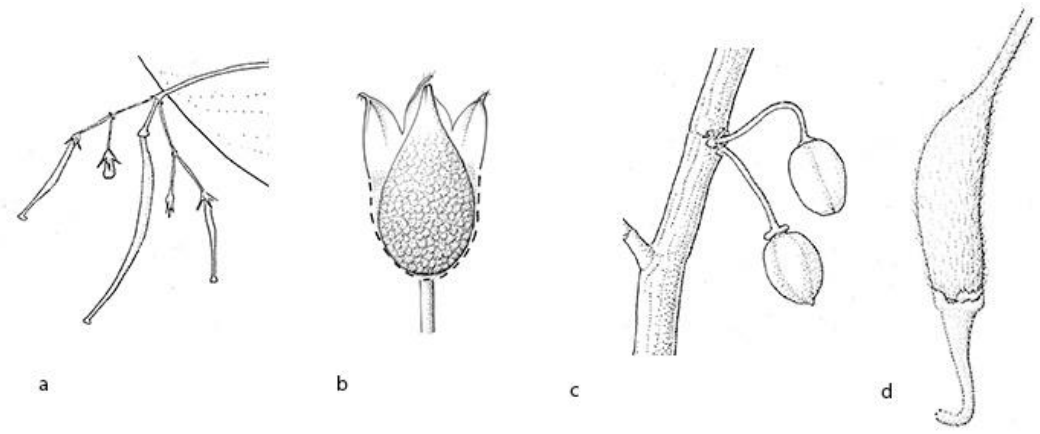


Fig. 2.8 Fruit types: a. linear b. ovoid c. sub-globose d. oblong

Indumentum

Indumentum on the vegetative parts of the plants, where present, is uniformly eglandular although it varies in density (Fig. 2.9).

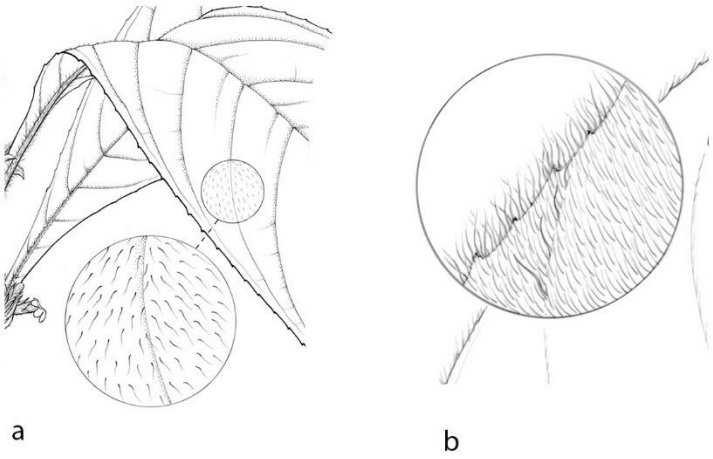


Fig. 2.9 Eglandular indumentum on leaves.

On the reproductive structures, however, most notably the ovary, style and the inside of the corolla lobes, there is variation in the type of indumentum present. The hairs are either eglandular or glandular (Fig. 2.10). The distinction between the two types is usually visible with a x 10 hand lens.

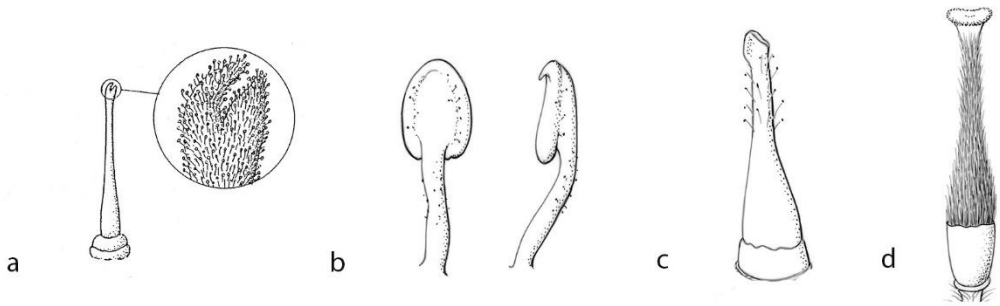


Fig 2.10 Indumentum types on reproductive structures: a-c. glandular hairs d. eglandular hairs

Taxonomic arrangement

The taxa in this account are listed alphabetically and have not been assigned to the sections used by C.B.Clarke (Clarke, 1883). His sections were established in the nineteenth century based on a fraction of the diversity of which we are now aware and are not widely used (Burtt, 2001; Bramley, 2003; Clark et al., 2013). Reference to the 14 monophyletic groups from Sulawesi referred to in the chapter on infrageneric structure are given following each description (Chapter Three). Further discussion of these groups including descriptions and a key is provided there.

Geography

Where possible, specimens have been georeferenced and the collections mapped. All collections are referred to the current province boundaries of North Sulawesi, Gorontalo, Central Sulawesi, South Sulawesi, West Sulawesi and South East Sulawesi. It is notable that although there are a small number of widespread species in Sulawesi, such as *C. polyneura, C. hypogaea* and *C. celebica,* many of the taxa are currently only known from a single province. This is particularly marked in the southern part of South Sulawesi where, from the Latimojong mountains south, the area appears to have its own distinct *Cyrtandra* flora and seven species found here are only recorded from this province, such as *C. purpureofucata, C. rantemarioensis, C. floccosa, C. sulcata* and *C. hispidula* and many of the widespread species such as *C. polyneura* and *C. hypoagaea* are notably missing. Twenty six of the Sulawesi taxa have been included in a recent biogeographic study of the genus in Malesia (Atkins et al., 2020) which shows that although two species, *C. polyneura* and *C. boliohutensis,* fall in a predominantly Sunda-shelf clade with species from Borneo and Sumatra, by far the majority of species fall in a clade which contains species from the Philippines, New Guinea and the Pacific suggesting a more Wallacean or eastern affinity to the Sulawesi taxa.

2.4 Keys and Descriptions

Cyrtandra J.R.Forst. & G.Forst., Char. Gen. Pl. 5 (1776).

Type species: *Cyrtandra biflora* J.R.Forst. & G.Forst. from French Polynesia.

The following generic description covers species known from Sulawesi.

Herbs, shrubs, rarely small trees or epiphytic climbers. *Stems* rounded to angular, hairy (with uniseriate, eglandular hairs) or glabrescent, sometimes woody. *Leaves* simple; opposite or in threes, sometimes appearing alternate; those of a pair or group subequal, or well developed but somewhat unequal in size, or with one leaf of a pair markedly reduced; petiolate or sessile; glabrous to densely hairy above, often more densely hairy below especially on midrib and veins; leaf bases occasionally markedly oblique, sometimes decurrent or auriculate; margins entire to serrate. *Inflorescence* cymose; axillary, geoflorous or cauliflorous; pedunculate or subsessile; flowers one to numerous. *Peduncle* with minute to large, sometimes connate, sometimes caducous, bracts. *Calyx* 5-lobed, tube long or short, deciduous or persistent in fruit. *Corolla* 5-lobed, limb weakly to strongly bilabiate, lobes recurved, spreading, erect or extending forwards, mouth open to strongly compressed laterally, usually white, sometimes yellow, purple, pink or red, sometimes with distinctive markings on lobes and throat. *Stamens* 2, filaments borne roughly midway in tube. *Staminodes* 2 or 3, borne roughly midway in tube. *Disc* cupular or unilateral, often persistent around ovary in fruit. *Ovary* superior, glabrous or hairy. *Style* glabrous or hairy. *Stigma* bilobed, peltate or capitate. *Fruit* ovoid, subglobose or oblong, hairy or glabrous, often tipped by a persistent style and sometimes with a persistent calyx in fruit. *Seeds* numerous, ellipsoid.

Key to the *Cyrtandra* species of Sulawesi

This key uses both vegetative and floral and fruit characters although emphasis has been given to vegetative characters wherever possible. A number of species have been keyed out in more than one position where they contain characters that are variable or difficult to interpret.

1a Some or all of the inflorescences on trailing stems running along the ground from the base of the plant.....2

1b Inflorescences not on trailing stems but in the axils of current leaves or occasionally at the base of the stem below the leaves.....6

2a Leaves narrow ovate to narrow oblong with crenate-serrate margins and 9–25 pairs of lateral veins; corolla glabrous externally ..... ***C. celebica***

2b Leaves narrow oblong to narrow obovate with serrate or lobed margins and 4–8 pairs of lateral veins; corolla sparsely hairy to hairy externally 3

3a Corolla white or red; leaves opposite (or occasionally in threes), those of a pair or group well developed although they may be somewhat unequal in size 4

3b Corolla pale yellow; leaves opposite one of each pair markedly reduced or both well developed but somewhat unequal in size..... ***C. luteiflora***

4a Trailing inflorescence stem slender (1mm or less in diameter), usually unbranched, appearing to be smooth; corolla > 15mm long; fruits smooth when dry.....5

4b Trailing inflorescence stem thick (up to 3mm diameter), often branching and appearing 'notched' at the site of old inflorescence bracts; corolla 8–15 mm long; fruits not smooth when dry but tesselate ..... ***C. hypogaea***

5a Corolla red, 15-20 mm long; inflorescence bracts up to 25 mm long; leaf base attenuate to very narrowly winged .....***C. rantemarioensis***

5b Corolla white with yellow and purple markings in throat, over 25 mm long; inflorescence bracts 1-2 mm long; leaf base acute .....***C. geocarpa***

6a Most or all of the inflorescences at the base of the stem significantly below the current leaves 7

6b Inflorescences usually opposite or in the axils of current leaves (fruits may be at the base of the stem below the leaves) 11

7a Epiphytic climber or shrub; leaf margins entire; fruits sub-globose; corolla purple to brown ..... ***C. purpurea***

7b Non-epiphytic herb, shrub or small tree; leaf margins not entire; fruits ovoid or narrow to broad ovoid to cylindrical; corolla white, yellow, pink or red 8

8a Leaves with 9–25 pairs of lateral veins, blade up to 40 cm long; corolla tubular, lobes strongly recurved, red ..... ***C. celebica***

8b Leaves with 4–7 pairs of lateral veins, blade up to 14 cm long; corolla funnelform, lobes spreading, white or pale red.....9

9a Corolla white, tube somewhat flushed pinkish externally, with yellow and purple markings in throat; inflorescence bracts 11-22 mm long; calyx ridged.....

.....C. boliohutensis

9b Corolla pale red or yellow; inflorescence bracts 2-4 mm long; calyx not strongly ridged 10

10a Corolla pale red, paler internally; calyx pale green; pedicels 5-7 mm; stigma bilobed....

.....***C. roseiflora***

10b Corolla yellow; calyx maroon; pedicels 30-40 mm; stigma peltate..... ***C. spectabilis***

11a Epiphytic climber; fruits sub-globose ..... ***C. purpurea***

11b Herb, shrub or small tree; fruits not sub-globose (can be ovoid to cylindrical).....12

12a Leaves up to 40 cm long with 9–25 pairs of lateral veins; corolla tubular, lobes strongly recurved, red; inflorescences axillary or on trailing stems from near the base of plant ***C. celebica***

12b Not as above 13

13a Peduncles long (3.5–8 cm long).....14

13b Peduncles subsessile or less than 3 cm long 16

(not including pedicels on a 1-flowered specimen; treat as a short peduncle)

14a Inflorescences with large bracts partially united and forming an involucre .....

.....***C. polyneura***

14b Inflorescences with small bracts not united.....15

15a Peduncles 3.5–8 cm long; fruits narrowly cylindric (2.5–3.5 cm x 1.5–2cm) .....

.....***C. tenuicarpa***

15b Peduncles 1.5–4 cm long; fruits ovoid (5 mm x 3 mm) .....***C. longirostris***

16a Inflorescence spicate, inflorescence axis up to 25 cm long.....***C. spicata***

16b Inflorescence not spicate (cymose, one to many-flowered, sessile or pedunculate, bracts free or united to form an involucre) 17

17a Upper surface of mature leaves with a significant covering of hairs 18

17b Upper surface of mature leaves glabrous or with scattered hairs/ciliate margins.....21

18a Leaves broad elliptic to ovate, over 9 cm wide; inflorescence bracts over 20 mm long .

.....***C. hispidula***

18b Leaves elliptic, ovate or narrow oblong, less than 8 cm wide; inflorescence bracts less than 15 mm long.....19

19a Inflorescence many-flowered, clustered in leaf axils; corolla 10-12 mm, white; leaves narrow oblong.....***C. albiflora***

19b Inflorescence 1 or 2-flowered; corolla 25-40 mm, not white, yellow or reddish; leaves narrow elliptic to ovate 20

20a Whole plant with dense, villous indumentum; leaves not drying dark brown .....

.....***C. mollis***

20b Whole plant with a rusty, floccose indumentum; leaves drying dark brown .....

.....***C. floccosa***

21a Leaf lamina decurrent (may be only winged towards base of petiole) or auriculate

.....22

21b Leaf lamina not decurrent to base of petiole 32

22a Leaf base auriculate; leaves deep glossy green.....***C. nitida***

22b Leaf base decurrent but not auriculate; leaves not deep glossy green 23

23a Inflorescence bracts linear (1–2mm wide) 24

23b Inflorescence bracts not linear (5–40mm wide).....26

24a Corolla less than 20 mm long; leaves with 17-20 pairs of lateral veins .....***C. sandei***

24b Corolla more than 30 mm long; leaves with 12 or fewer pairs of lateral veins 25

25a Corolla white; leaves with 3–5 pairs of lateral veins; stems striate, not scaley.....

.....***C. jellesmani***

25b Corolla yellow with red stripes on the lobes; leaves with 9–12 pairs of lateral veins; stems tesselate, scaley..... ***C. fasciata***

26a Leaves less than 5 cm wide at widest point 27

26b Leaves 5 cm or wider at widest point.....28

27 a Shrub or small tree; leaves narrow oblong to lorate, over 14 cm long; inflorescence bracts dull red, c. 30 mm long; corolla c. 35-45 mm long.....

..... ***C. rubribracteata***

27b Herb; leaves narrow elliptic or oblong, less than 8 cm long; inflorescence bracts green, less than 10 mm long; corolla c. 15 mm long ..... ***C. hekensis***

28a Calyx white or pinkish; corolla with lower lip strongly elongated and recurved .....

.....***C. longistamina***

28b Calyx green or red; corolla with lower lip not strongly elongated and recurved.....29

29a Inflorescence bracts less than 10mm wide 30

29b Inflorescence bracts 20-25 mm wide 31

30a Leaves with 8–11 pairs of lateral veins; corolla pink, 15–18 mm long.....***C. hendrianii***

30b Leaves with 11–18 pairs of lateral veins; corolla white with yellow markings, over 40 mm long .....***C. flavomaculata***

31a Flowers small: calyx less than 10 mm long, corolla less than 15 mm long. Herb or shrub to 1 m .....***C. polyneura***

31b Flowers large: calyx greater than 15 mm long, corolla greater than 30 mm long. Shrub or small tree to 7 m ..... ***C. kinhoii***

32a Leaf margins distinctly serrate or lobed 33

32b Leaf margins not distinctly serrate (can be subentire to serrulate) 40

33a Leaves up to 2 cm long with 3–4 pairs of lateral veins..... ***C. serratifolia***

33b Leaves 4–16 cm long with 4–9 pairs of lateral veins 34

34a Leaf broad elliptic to ovate, more than 8 cm wide.....***C. hispidula***

34b Leaf elliptic, less than 6 cm wide 35

35a Calyx ridged; bracts c. 20 mm long.....***C. boliohutensis***

35b Calyx not ridged; bracts less than 7 mm long.....36

36a Leaves opposite and more or less equal; petiole 12-25 mm; calyx 19-34 mm; leaves drying dark brown..... ***C. floccosa***

36b Leaves opposite with some on the plant highly reduced, sometimes appearing alternate; petiole 3-10 mm; calyx 6-15 mm; leaves not drying dark brown.....37

37a Leaf margins deeply incised with 3-7 lobes along each side ..... ***C. kjellbergii***

37b Leaf margins serrate 38

38a Corolla white or pale yellow, c. 20 mm long ..... ***C. balgooyi***

38b Corolla pale red to deep pink, over 25 mm long 39

39a Corolla narrowly funnel-shaped, lobes not recurved.....***C. roseiflora***

39b Corolla with narrow tube in basal half becoming wider and pouched in apical half, narrowing again at mouth; lobes strongly recurved.....***C. purpureofucata***

40a Leaves with 17–19 pairs of lateral veins.....***C. multinervis***

40b Leaves with 4–12 pairs of lateral veins.....41

41a Both leaves of a pair well developed if somewhat unequal in size***.....*** 42

41b Leaves usually appearing alternate or with one leaf of a pair highly reduced (very occasionally both leaves of a pair on a predominantly anisophyllous plant may be well developed)43

42a Inflorescences not subsessile; peduncles 15–40 mm long.....***C. longirostris***

42b Inflorescence subsessile; peduncles less than 5 mm long.....***C. sulcata***

43a Most leaves over 4 cm wide at the widest point (up to 6.5cm wide); peduncle 5-15 mm ..... ***C. bruteliana***

43b Most leaves under 4 cm wide at the widest point (1–4 cm wide); peduncle less than 5 mm 44

44a Leaves with more than 6 pairs of lateral veins.....45

44b Leaves with 6 or fewer pairs of lateral veins.....47

45a Tertiary venation barely visible (on herbarium specimens); lateral veins running straight out to margin without looping upwards; corolla white with purple markings, 19–20 mm long ..... ***C. gambutensis***

45b Tertiary venation easily visible (on herbarium specimens); lateral veins looping upwards and sometimes joining vein above; corolla white, less than 15 mm long.....46

46a Reduced leaf, in an anisophyllous pair, cordate; inflorescence bracts 2–4 mm long, 1-4(-7) flowers per inflorescence ..... ***C. widjajae***

46a Reduced leaf, in an anisophyllous pair, usually scale-like; inflorescence bracts 6–10 mm long, usually 7-8 flowers per inflorescence..... ***C. sopuensis***

47a Calyx short relative to corolla (1/4 to 1/3 corolla length), calyx (including lobes) less than 5mm long .....***C. parvicalyx***

47b Calyx at least half corolla length, calyx (including lobes) 7–13 mm long 48

48a Pedicels up to 5 mm long; calyx evenly 5-lobed, 10-13 mm long; corolla white with purple markings .....***C. engleri***

48b Pedicels (5-)15-30 mm long; calyx with three upper lobes united into a shallowly notched limb, and two lower lobes similary united, 7–10 mm long; corolla creamy white to pale yellow without markings.....***C. gorontaloensis***

Cyrtandra albiflora Karton. & H.J.Atkins**,** Edinburgh J. Bot. 75(2): 174 (2018) – Type: Indonesia, Central Sulawesi, Sumber Agung, Sungai Spa, 92 m, 24 ii 2004, *Hendrian, Newman, Scott, Saleh, & Supriadi 848* (holotype E; isotype BO). **Fig. 2.11**

Shrub to 60 cm in height. ***Stems*** striate, densely villose hairy on young growth, hairs up to 3 mm long, indumentum less dense on older growth. ***Leaves*** opposite, subequal (with occasional whorl of smaller leaves on cultivated plants); petiole c. 2 cm long, hairy, narrowly winged; blades 17–22.5 x 5.1–7.7 cm, narrow oblong, apex acuminate, base attenuate, margin serrulate; 9–11 pairs of lateral veins and reticulate tertiary venation, light green and hairy above, appearing whitish and hairy below, most densely so on midrib and veins. ***Inflorescences*** axillary, subsessile, with c. 8–10 flowers at various stages of development; bracts green, caducous, 10–11 x 5 mm, linear–lanceolate, hairy on both surfaces, most densely so along margins; bracteoles 6–8 mm long, linear, hairy internally and along margins; pedicels 2–3 mm long, densely hairy. ***Calyx*** tubular, green, 5–6 mm long, lower lip 2–lobed, lobes short-acuminate, c. 3 mm long, upper lip divided very briefly at apex, densely hairy externally. ***Corolla*** white, 10–12 mm long, widening gradually to mouth, mouth oblique, upper lobes rounded erect to slightly recurved, 1.5 x 2 mm, lower and lateral lobes more elongate, spreading to slightly recurved, 3 x 2.5 mm, hairy externally and with glandular hairs internally, on lobes and in mouth. ***Stamens*** with filaments c. 1 mm long, attached 5–6 mm from base of corolla, glabrous; anthers c. 1 mm long, glabrous, cohering at apices; staminodes 3, all less than 0.2 mm long. ***Gynoecium*** 5.5–6 mm long; disc cupular with undulate margin, 1 mm long, glabrous; ovary glabrous; style glandular hairy; stigma slightly bilobed, lobes small and held upright. ***Fruits*** ovoid, drying dark brown, glabrous, verrucose, 5–6 x 2–3 mm, base of style and calyx persistent.

Distribution. Central Sulawesi: Luwuk (Fig. 2.14).

Habitat and ecology. Disturbed lowland forest in a limestone area at an altitude of 92–220m.

Etymology. This species is named for its white flowers.

Proposed IUCN conservation category. *Cyrtandra albiflora* is known from a single mountain from which two collections were made on the same trip in 2004 at altitudes of 92 and 220m. This lack of specimens precludes estimations of EOO but the species has an AOO of 8 km^2 (Bachman et al., 2011)(map in Appendix 2.1). According to Cannon et al. 2007, lowland forest is one of the most threatened habitats on the island and there are no protected areas in this part of Sulawesi (UNEP-WCMC & IUCN, 2019). Until more intensive botanical exploration can be made in this area it is assumed that this species is restricted to the Type locality. Following Kartonegoro et al. (2018), it is recommended that this species is categorised as Vulnerable (VU) using the criteria VUD2 as it is a population with a very restricted number of locations in an area without protection and in a habitat that is known to be threatened (Cannon et al., 2007).

Additional specimens examined. **Central Sulawesi:** Luwuk, Mt Hek, Sungai Spa, 24 ii 2004*, Scott, S. 04-307*, grown on at RBGE as accession 20040645A, vouchered as *Scott* 509 (E).

Sulawesi Group: 5 (Atkins et al., Chapter 3).

Notes. This species is similar to *Cyrtandra hendrianii*, also from Gunung Hek, in being a shrub with subequal, decurrent leaves and many-flowered axillary inflorescences. It can be distinguished, however, by its white corolla (vs corolla pink), green calyx (vs calyx red), densely villous stems and leaves (vs stems and leaves more or less glabrous) and linear-lanceolate bracts 10–11 mm long (vs oblong-lanceolate bracts, 25–35 mm long).

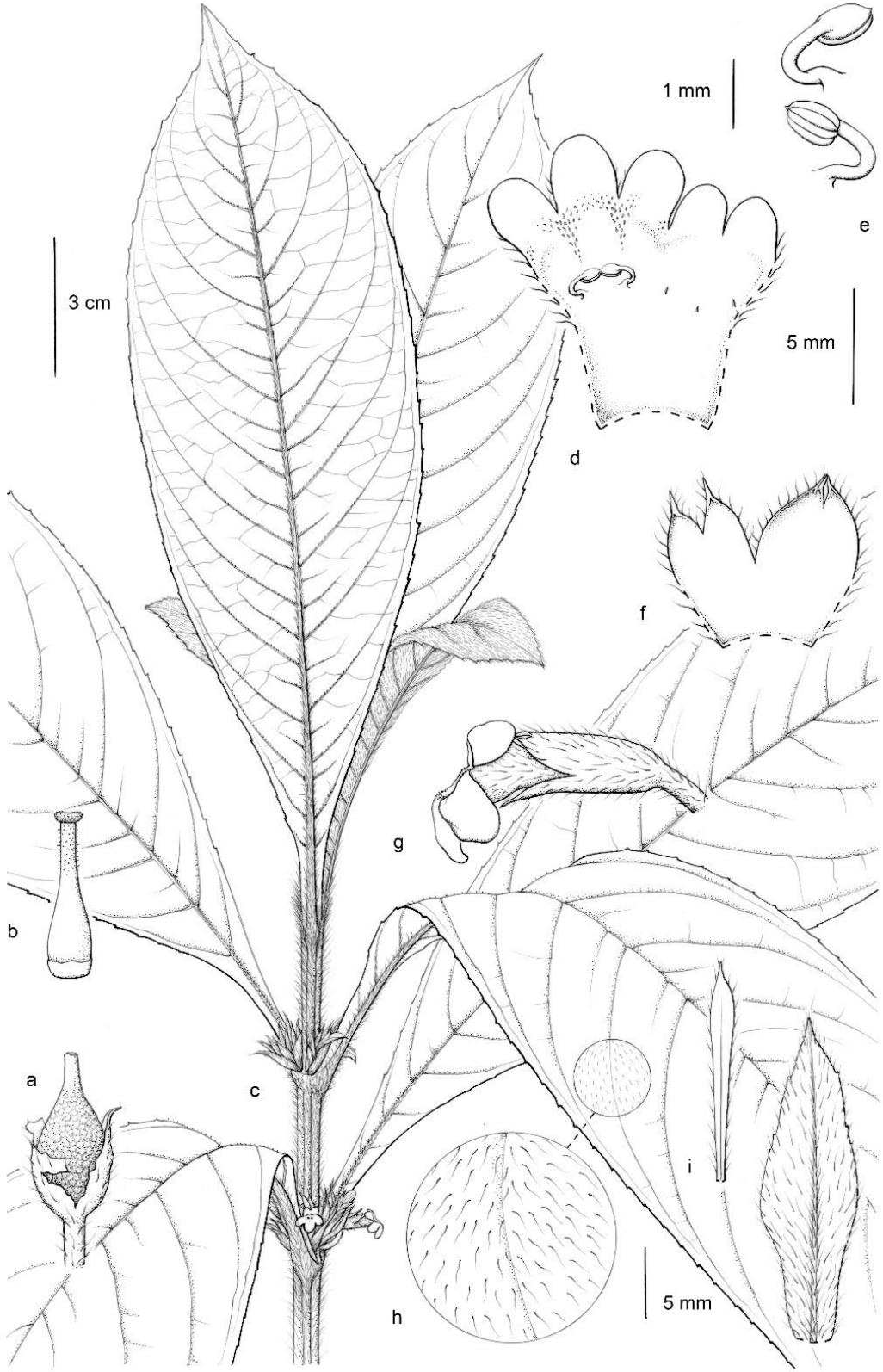


Fig. 2.11 Line illustration of *Cyrtandra albiflora* showing a. Fruit and calyx b. Gynoecium including disc c. Habit d. Opened corolla showing position of stamens and staminodes e. Anthers f. Opened calyx showing inner surface g. Side view of corolla h. detail of upper leaf surface i. Bracts and bracteoles. Drawn by Claire Banks from *Hendrian* et al. 848. Reproduced from Kartonegoro et al. (2018).

Cyrtandra balgooyi H.J.Atkins & Karton**. sp. nov.** ined.

Similar to *Cyrtandra widjajae* Karton. in having strongly anisophyllous leaves and densely hairy calyces, corollas and fruits but differing in leaf margin (serrate in *C. balgooyi* vs subentire in *C. widjajae*), number of lateral vein pairs (4–5 pairs in *C. balgooyi* vs 8–14 pairs in *C. widjajae*) and corolla length (corolla 20 mm long in *C. balgooyi* vs corolla 12–15 mm long in *C. widjajae*). – Type: Sulawesi, Danau Tambing, 23 v 1979, *van Balgooy* 3469 (holotype L; isotype BO, E). **Fig. 2.12**

Shrub or small tree to 2.5 m in height. ***Stems*** striate, sparsely hairy, densely coarse-hairy on young growth. ***Leaves*** opposite; one leaf of a pair markedly reduced or appearing alternate; petiole 5-6 mm long, hairy; blades of larger leaves 4–7(-8) × 1.5–2.5(-3) cm, elliptic to narrow obovate, apex acuminate, base acute, not decurrent, more or less symmetrical, margin coarsely serrate; 4–5(-6) pairs of lateral veins which loop upwards and join eventually with the vein above with short veins running out to adjacent teeth, tertiary venation reticulate, subglabrous to sparsely hairy above, sparsely hairy below, more densely so on midrib and veins. *Reduced leaves* 1-5 mm long, cordate or with the blade barely developed. ***Inflorescences*** subsessile to very shortly-pedunculate in the leaf axils, 1–2-flowered; peduncle up to 1 mm long, densely hairy; bracts 1–2 × 1 mm, linear, hairy; pedicels up to 6 mm long, densely hairy. ***Calyx*** very pale green to white, campanulate, 10–12 mm long, more or less evenly five-lobed or with two sets of lobes tightly adpressed at apices appearing almost three-lobed, initally enclosing the corolla, lobes subulate, 5 mm long, densely coarse-hairy externally. ***Corolla*** creamy white to pale yellow, 20 mm long, more or less parallel-sided, widening gradually to mouth, lobes spreading not strongly recurved, lobes 3–4 × 3–4 mm, glandular-hairy internally at base of lobes, densely eglandular hairy throughout externally. ***Stamens*** with filaments 2.5–3 mm long, attached 7-9 mm from base of corolla, anthers 1 mm long, cohering at apices before dehiscence; staminodes 2 mm long. ***Gynoecium*** 12–13 mm long; disc cupular with lobed margin, 1 mm long, glabrous; ovary and style densely eglandular hairy; stigma peltate, slightly bilobed, 2 mm across. ***Fruits*** ovoid, densely hairy, 6 × 4 mm (immature?), calyx not or partially persistent, base of style persistent.

Distribution: Central Sulawesi, in and around Lore Lindu National Park (Fig. 2.14).

Habitat and ecology. Upland and montane forest at an altitude of 1333–2355 m.

Etymology. This species is named after Dr M.M.J. van Balgooy of the Nationaal Herbarium Nederland who has contributed so much to our knowledge of the flora of southeast Asia and was the collector of the type specimen.

Proposed IUCN conservation category. The EOO of this species is 444 km^2 and the AOO is 20 km^2 (based on a 2 x 2 km grid cell size) under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). Most of the collections fall within the boundaries of Lore Lindu National Park (UNEP-WCMC & IUCN, 2019) and, as such, should receive some protection. They are also at relatively high altitude in the slightly less threatened upland and montane forest types (Cannon et al., 2007). A category of Least Concern is suggested for this species.

Additional specimens examined: **Central Sulawesi:** Gunung Nokilalaki, track to shelter 2, 24 vii 2018, *Ardi* WI225 (KRB); Lore Lindu National Park, Tamping lake, 4 viii 2018, *Ardi* WI296 (KRB); Summit of Mt Ngilalaki, 9 vii 1939, *Bloembergen* 3986 (A, BO); Mt Nokilalaki, 6 iii 2008, *Cicuzza* 787 (E); ibid, 18 iii 2008, *Cicuzza* 936 (E); Lore Lindu National Park, Uwei Balamba, 21 ii 2011, *Culmsee* y2077 (BO, E). Sopu Valley, c. 80 km from Palu, 29 iv 1979, *Hennipman* 5110 (A, E, L).

Sulawesi Group: 14 (Atkins et al., Chapter 3).

Notes. Cyrtandra balgooyi is part of a group of seven species that share the characters of strongly anisophyllous leaves; white or light yellow corollas and densely hairy calyces, corollas and fruits. The others in the group are *C. gambutensis, C. gorontaloensis, C. balgooyi, C. widjajae, C. parvicalyx* and *C. sopuensis. Cyrtandra balgooyi* is currently only known from a small area of Central Sulawesi. The other two species in the group from this area are *C. sopuensis* and *C. widjajae.* This new species can be distinguished most easily from these by its coarsely serrate leaf margin, smaller number of lateral vein pairs (4-5 pairs vs 7-14 pairs) and larger flowers (20 mm long vs .11—15 mm long).

Fig. 2.12 Plate of *Cyrtandra balgooyi* showing a. stem and side view of flower b. front view of flower. Photos: Fabian Brambach. *Culmsee* y2077.

Cyrtandra boliohutensis Karton. & H.J.Atkins, Edinburgh J. Bot. 75(2): 178 (2018) - Type: Sulawesi, Gorontalo Province, Mt Boliohutu, 24 iv 2002, *Atkins, Mendum, Newman, Hendrian & Sofyan* 188 (holotype BO; isotype E and isotype L). **Fig. 2.13**

Branching herb to 1 m in height. ***Stems*** slender, striate, sparsely hairy. ***Leaves*** opposite, both members of a pair well developed but somewhat unequal in size or with one leaf of a pair markedly reduced, sometimes appearing alternate; petioles 1.2–2.5 cm long, hairy; blades 7–14 × 3–5 cm, oblong to narrow oblong, occasionally somewhat rhomboid, apex acuminate, base attenuate, slightly asymmetrical, margin serrate; 4–6 pairs of lateral veins, curving and running out to margin, subglabrous above, sparsely hairy below, more densely so on midrib and veins; reduced leaves (where present) 4–5 mm long, scale–like, occasionally cordate. ***Inflorescences*** subsessile to shortly pedunculate in leaf axils or at base of stems in the axils of fallen leaves, 1–2–flowered; peduncle 1–2 mm long, hairy; bracts elliptic or oblong, glabrous, greenish–brown, 11–22 × 8–10 mm, partly enclosing calyx at the base, two lobed at apex or divided almost to base, sparsely hairy; bracteoles

single, oblong, glabrous, green-brown, 10–16 x 5–6 mm; pedicels 2–5 mm long, sparsely hairy. ***Calyx*** tubular, ridged, green becoming dark red along ridges, 17–25 mm long, evenly 5-lobed, lobes 2 mm long, triangular, acuminate at apex, sparsely hairy externally. ***Corolla*** white, tube somewhat flushed pinkish externally, yellow in throat with fine, purple spots on the inside of lobes, 35–65 mm long, narrowly funnel–shaped, flattened laterally, brown eglandular hairy externally, lobes spreading not recurved, 9–10 × 5–8 mm. ***Stamens*** with filaments 8–12 mm long, attached 20–30 mm above base of corolla; anthers 1.5–3 mm long, coherent at apices, with a fringe of hairs at the base of each anther; staminodes 3, 4–7 mm long. ***Gynoecium*** 23–35 mm long; disc cupular with lobed margin, 2 mm long, glabrous; ovary glabrous; style glabrous at base, eglandular hairy towards stigma; stigma peltate, slightly bilobed, 2 mm across. ***Fruits*** oblong to narrow ovoid, green or brown-green, glabrous, verrucose, 10–25 × 2–4 mm; calyx not or only partially persistent, base of style persistent.

Distribution. Gorontalo and Central Sulawesi (Fig. 2.14).

Habitat and ecology. Lowland to upland forest at an altitude of 50–1400 m.

Etymology. This new species is named after one of the mountains on which it was collected.

Proposed IUCN conservation category. The EOO of this species is 28,566 km^2 and the AOO is 16 km^2 (based on 2km x 2 km grid cell size) under the B criteria (Bachman et al., 2011). All of the collections fall within protected areas: the Nantu Sanctuary Forest, the Mt Sojol Nature Reserve and the Lore Lindu National Park (UNEP-WCMC & IUCN, 2019). Many of the collections are at relatively low altitudes where the general threat to this habitat type on the island is known to be high (Cannon et al., 2007; Thomas et al., 2011). As all of the collections fall within protected areas, a category of Least Concern is suggested for this species.

Additional specimens examined. **Gorontalo.** Mt Boliohutu, 320m, 24 iv 2002, *Atkins* et al. 190 (BO, CEB, E, K, L); Mt Boliohutu, 320m, 24 iv 2002, *Scott, S.* 02-126, grown at RBGE as accession 20021906A, vouchered as *Scott* 505 (E);

Central Sulawesi. Pangi Binangga, Uwe lutu, 20 vii 2018, *Ardi* WI212 (KRB); Gunung Nokilalaki, 24 vii 2018, *Ardi* WI224 (KRB); Ponoh, 3 km NE of Toro village, 12 xii 2007, *Cicuzza* 549 (E); Mt Sojol, 1400 m, 27 ii 2000, *Mendum* et al. 00196 (BO, CEB, E, L).

Sulawesi Group: 1 (Atkins et al., Chapter 3).

Notes. This species is morphologically similar to a group of Bornean species which includes *C. basiflora* C.B.Clarke and *C. mendumiae* Hilliard & B.L.Burtt. They all have large flowers with long, soft hairs, flower at the base of the stem, slightly rhomboid leaves and a strongly ridged calyx. This species is most easily distinguished from these by the distinctive tuft of hairs on the base of the anthers and the short peduncles, only 1-2 mm long in *C. boliohutensis* and 5-20 mm long in the Bornean species.

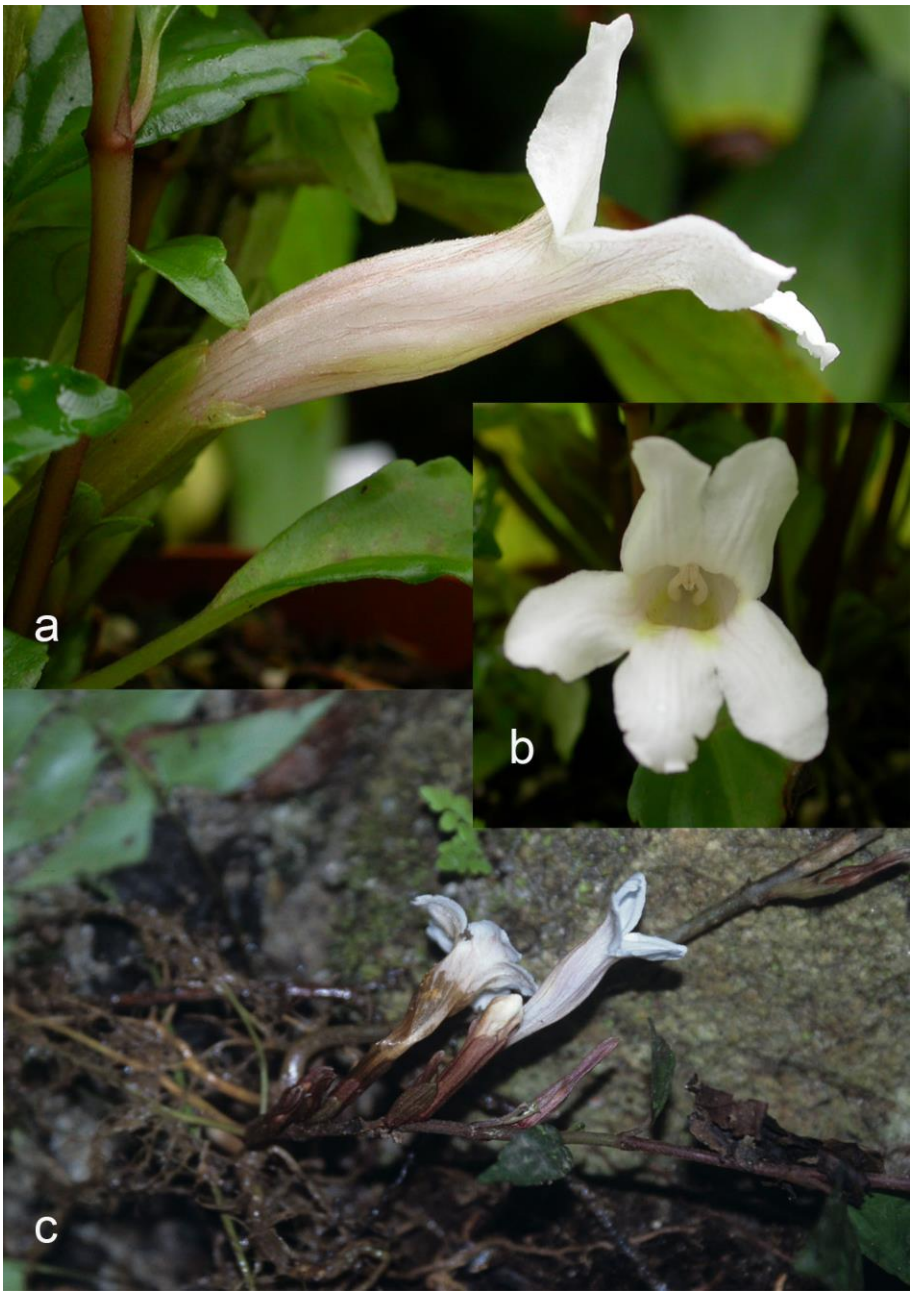


Fig. 2.13 Plate of *Cyrtandra boliohutensis* showing a. side view of flower b. front view of flower c. habit. Photos: a&b: Steve Scott c: Hannah Atkins. Reproduced from Kartonegoro et al. (2018).

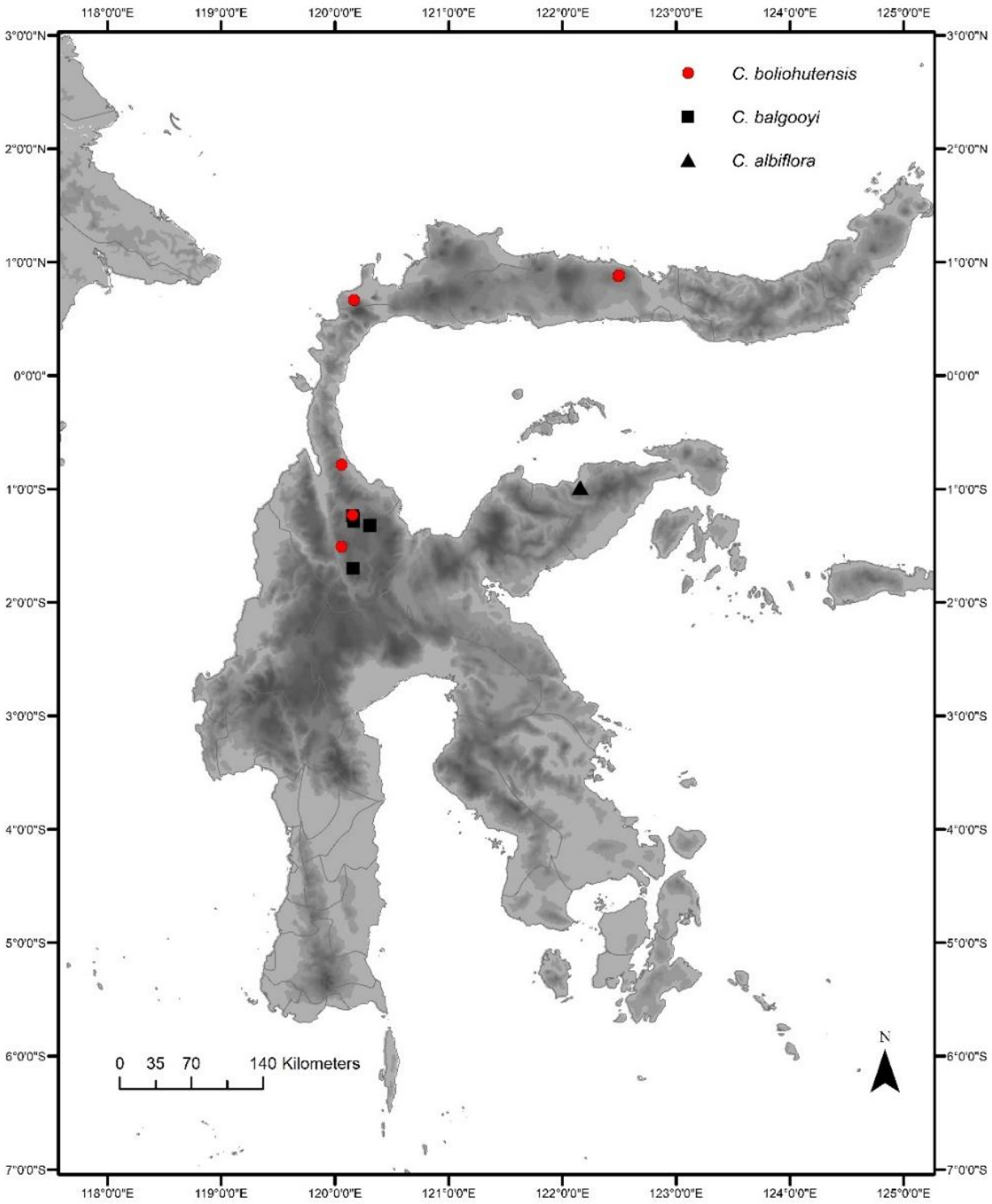


Fig. 2.14 Distribution of *Cyrtandra boliohutensis* (red circle), *C. balgooyi* (black square) and *C. albiflora* (black triangle).

Cyrtandra bruteliana Koord., Meded.'s Land. Plantent.19: 550, 627 (1898). – Type: Celebes [Sulawesi], Gunung Lolomboelan, Minahassa, 6 iv 1895, *Koorders* 17183 (lectotype L hic desig.; isolectotype BO). **Fig. 2.15**

Branching shrub to 2(–3) m in height. ***Stems*** striate, sparsely hairy, more densely so on young growth. ***Leaves*** appearing alternate, occasionally opposite with one of each pair highly reduced; petiole 10–15 mm long, sparsely hairy to hairy; blades of larger leaf (6–)12–18 cm × (2–)4–6.5 cm, narrow elliptic to narrow-oblong, apex long-acuminate to 15mm, acute and slightly asymmetric at base, margins subentire to serrulate; 7–10 pairs of lateral veins, veins prominent, curving upwards and running out to margin, tertiary venation faint, subglabrous above, sparsely hairy below, more densely so on midrib and veins. ***Inflorescences*** axillary, pedunculate in leaf axils or opposite leaves, 3–6(–8)-flowered; bracts green, lanceolate, not connate, 10–15 mm × 5 mm, sparsely hairy to hairy; bracteoles green, lanceolate, hairy, up to 7 mm × 3 mm; peduncles 5–15 mm, densely hairy; pedicels 3–5 mm, hairy. ***Calyx*** light green, evenly 5-lobed, 7–8 mm long, sparsely to densely hairy, lobes acuminate at apex, 5 mm long. ***Corolla*** white or yellow, sometimes with a greenish centre, more or less parallel-sided, widening only slightly to mouth, 12–13 mm long, lobes spreading, not strongly recurved, upper lobes 2 mm × 3 mm, lower lobes 3 mm × 3 mm sparsely eglandular hairy externally. ***Stamens*** with filaments 3 mm long, attached 5 mm above base of corolla, glandular hairy; anthers less than 1 mm long, connected at tips before dehiscence; staminodes less than 1 mm long. ***Gynoecium*** 8 mm long; disc 1 mm long, cupular with undulate margin, glabrous; ovary subglabrous to sparsely glandular hairy; style glandular hairy for whole length; stigma capitate with two short, blunt lobes, c. 0.5 mm across. ***Fruit*s** 5–10 mm × 3–5 mm, broad-ovoid to sub-globose, sparsely hairy, green, remnants of calyx persistent, style and stigmas also often persistent, bracts and bracteoles sometimes persistent.

Distribution. North Sulawesi, Central Sulawesi, South East Sulawesi. (Fig. 2.17).

Habitat and ecology. This species has been collected in forest over a wide altitudinal range from 500–1400 m but with most of the collections from altitudes over 1000 m in hill and upland forest.

Etymology. This species was named by Koorders after Dr Brutel de la Rivière who assisted him with the publication of his comprehensive paper on fieldwork and botany in Minahasa (Koorders, 1898).

*Proposed IUCN conservation category.*This species has an EOO of 162,078 km^2 and an AOO of 56 km^2, using a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). Given the relatively high numbers of recent collections from both the north and southeast of the island, and the fact that at least some of the collections are from the protected areas of Gunung Ambang and Gunung Sojol Nature Reserves and Bogani Nani Wartabone (formerly Dumoga Bone) National Park (UNEP-WCMC & IUCN, 2019), a provisional assessment of Least Concern is suggested for this species.

Additional specimens examined: **North Sulawesi**. Minahasa, Mt Tangkoko, 28 vi 1954, *Alston* 16129 (A, BM, BO); Gunung Ambang Nature Reserve, 2 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK39 (BO, E); Leleasan, Wiau complex, 30 vi 1956 *Forman* 342 (BO, K, L); Gunung Manimporok, 8 ii 2009, *Girmansyah* 1127 (BO); Goeroepahi, Urskogen, 14 iv 1917, *Kaudern* 59 (L, S); Lolomboelan by Pakoe-oere, 6 iv 1895, *Koorders* 17183 (BO, L); Minahasa, *Koorders* 17199 (BO); Dumoga Bone National Park, Bolaang Mongondow, vicinity of G. Sinombayuga, 30 ix 1991, *Milliken* 1132 (L);

Central Sulawesi. Pangi Binangga, Uwe lutu, CA, 20 vii 2018, *Ardi* WI211 (KRB); Balukang, Siboang Desa, Dusun Maros, Camp 1, Puncak Pinimoang, east of Kampung Sipaton on the way to Gunung Sojol, 20 vii 2002 *Brown, Craven, Juswara & Ramadhanil* 82 (BO, CEB n.v., E, L);

South East Sulawesi. Kolaka, Mt Mekongga, 19 iii, 2006, *Girmansyah* 584 (BO); Rante Angin subdistrict, Tinukari village, Mekongga mountain range, 7 viii 2009, *Hidayat, Santika & Hapid* AH 4217 (BO, E); B. Watoewila, 24 iii 1929, *Kjellberg* 1020 (BO, S); Hutan Silui, Kecamatan Uluiwoi, Kolaka, 15 v 2008, *Santika* YS 343 (BO, E, L).

Sulawesi Group: 13 (Atkins et al., Chapter 3).

Notes. This species is distinctive in Sulawesi due to its combination of apparently alternate leaves with faint tertiary venation and broad ovoid to sub-globose fruits with persistent calyces. It is similar morphologically to *C. callicarpifolia* Elmer from the Philippines (Elmer, 1910), particularly in the form of the inflorescence, although the leaves are smaller and narrower with serrate margins in the Philippine species.

Despite the relatively large number of collections, it was only possible to take detailed floral measurements from one specimen (*Kaudern* 59) as most of the collections were fruiting only.

Koorders did not specify a type for this species, so Koorders' own collection, *Koorders* 17183, is designated here as the lectotype.

Fig. 2.15 Plate of *Cyrtandra bruteliana* showing a. infrutescence b. side view of flower c. stem and leaves. Photos: Deden Girmansyah (B) [Girmansyah 1127].

Cyrtandra celebica Blume in Bijdr.: 772 (1826). – Type: Celebes [Sulawesi], in monte Lokkon, Oct 1821, *Reinwardt* 1541 (lectotype L. hic. desig.). - *Rhynchocarpus coccineus* Reinwardt ex de vriese in Pl. Ind. Bat. Orient. 11 (1856). nom. inval. - *Cyrtandra coccinea* var. *celebica* (Blume) C.B.Clarke syn. nov., A.DC. & C.DC., Monogr. Phan. 5: 256 (1883).

Cyrtandra rhizantha Kraenzlin syn. nov., J. Linn. Soc. 37: 277 (1906). - Type: Celebes [Sulawesi], Forêt a l'entrée de la vallée du Tiram, 23–25.8.1876, *de la Savinierre* 138 (holotype K).

Shrub or small tree to 10 m in height, usually much less. ***Stems*** subglabrous, woody, occasionally with prop roots. ***Leaves*** opposite or sometimes in threes; those of a pair or group well developed but somewhat unequal in size; petioles 2.5–6(–11) cm, glabrous, often warty at base; blades 8–40 cm × 6–18.5 cm, narrow-ovate to narrow-oblong, acuminate at apex, markedly oblique at base, not decurrent, margin subentire to crenate-serrate; 9–25 pairs of lateral veins, curving upwards and running out to margin, tertiary venation reticulate, sometimes quite obscure; sparsely hairy above, glabrous to sparsely hairy below, including midrib and veins. ***Inflorescences*** cauliflorous, often near base of stem, or occasionally in leaf axils, many-flowered; inflorescence stem pendulous or trailing often from a single point and then branching, appearing slightly notched from the remains of old bracts and bracteoles; bracts and bracteoles 10–15 mm × 5–10 mm, ovate, glabrous to sparsely hairy, connate sometimes only at base, sometimes to three quarters length, soon caducous. ***Calyx*** tubular, slightly bilabiate, dark red or green, 12–20 mm long, lobes triangular, shortly acuminate at apex, three upper lobes very briefly divided, c. 3 mm x 2 mm, two lower lobes slightly longer, c. 5 mm x 4 mm, glabrous externally. ***Corolla*** red, 20–25(-35) mm long, tubular, very narrow towards base, mouth oblique with lower and lateral lobes recurved and folded under themselves thus appearing very small, c. 1mm × 4 mm, upper lobes extending forwards, c. 2 mm × 4 mm, more or less glabrous externally with a scattering of short glandular hairs towards the lobes; lobes glandular hairy internally. ***Stamens*** with filaments 8–12 mm long, attached 11–18 mm from base of corolla, cream or pinkish, glabrous; anthers brown or cream, 2-3 mm long, connected at tips before dehiscence; staminodes 1–1.5 mm long. ***Gynoecium*** 20–30 mm long; disc cupular, slightly wider at base, sometimes with one side slightly lower than the other and slightly undulate margin, glabrous, 2 mm long; ovary glabrous; style glandular at the top of the style near the stigma, glabrous towards the ovary; stigma peltate, slightly bilobed, 2.5 mm across, green, exserted beyond the mouth of the corolla at maturity. ***Fruits*** narrow ovoid to oblong, 10–15 mm × 3–5 mm, glabrous, green when unripe, calyx not persistent, base of style persistent.

Distribution. North, Central, West and South East Sulawesi (Fig. 2.17)

Habitat and ecology. Lowland to montane forest, often on vertical banks at an altitude of 50–1600 m

Etymology. This species is named after the island of Sulawesi using its former name Celebes.

Proposed IUCN conservation category. The EOO of this species is 210,408 km^2 and the AOO is 116 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). This species is one of the most widespread on the island with a very wide altitudinal range from 50 to 1600m and collected on a number of recent expeditions (in 2003, 2008, 2009, 2011 and 2016). For these reasons, it is given a category of Least Concern.

Additional specimens examined: **North Sulawesi**. Tomohon, 5 vi 1954, *Alston* 15665 (A, BM, BO); Above Kelelonde, Soputan Mountains, 16 v 1954, *Alston* 15859 (A, BM, BO); Winowangan, 4 km E of Menado, 3 vii 1954, *Alston* 16189 (A, BM, BO, L, S); Mt Masarang, 4 xii 2003, *Ambriansyah* AA2656 (BO); Manado, Malalayang waterfall, 31 i 2019, *Ardi* WI393 (KRB); Bolaang Mongondow, Tapakolintang area, 29 x 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK12 (BO, E); Kasingolan River, 30 x 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK15 (BO, E); Gunung Ambang Nature Reserve, 2 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK49 (BO, E); Tondano, 1923, *Boesveld* (BO); Mt Mahawae, Tomohon, 23 v 1956, *Forman* 225 (BO, L); Wagio Crater, Mt Mahawae, Tomohon, 4 vii 1956, *Forman* 385 (BO, L); Sangihe & Talaud, Tabukan Selatan, 27 ix 1998, *Hicks* 87 (K); Sangihe & Talaud, between Ganding peak and Batungbakara peak, 12 iv 1999, *Hicks* 225 (E, K); Minahasa, 1894-5, *Hose* 799 (BM, K); Sangi & Talaud Isles, Karakelang, slope of G. Datua, 2 v 1926, *Lam* 2744 (BO, L); Tomohon, 9 i 1895 *Koorders* 17179B (BO, L); Lokon, 7 i 1895, *Koorders* 17184B (BO, L); Menado, 28 xii 1894, *Koorders* 17198B (BO, L); Tomohon, 6 i 1895, *Koorders* 17201B (BO); Tondano, 1923, *Kruyff* 18 (BO); Mt Soputan, 11 x 1973, *de Vogel* 2497 (A); Bolaang Mongondow, Dumoga Bone National Park, Gunung Mogogonipa, 12 iv 1985, *de Vogel & Vermeulen* 7114 (K, L); Gunung Ambang Nature Reserve, Bolrang Solfatara area, 19 iv 1985, *de Vogel & Vermeulen* 7300 (K, L); Manado, ii 1923, *Wisse* 101(BO);

Central Sulawesi. Lore Lindu National Park, 29 vii 2018, *Ardi* WI248 (KRB); Luwuk area, inland from Batui, 15 x 1989, *Coode* 5944 (BO, K, L, SING); Luwuk district, Bunta subdistrict, Sumber Agung, Gunung Hek, Sungai Hek, 25 ii 2004, *Hendrian*, *Newman, Scott, Saleh & Supriadi*. 896 (E); Area of Mt

Nokilalaki, SE of Lake Lindu, 3 v 1975, *Meijer* 9981 (L); Top of pass from Palu to east coast, 23 ii 2000, *Mendum, Argent & Hendrian* 00129 (E); Gunung Hek, 14 iv 2008, *Thomas & Ardi* 08-50 (E, BO, CEB n.v.); Gunung Katopas, 7 v 2008, *Thomas & Ardi* 08-68 (E, BO, CEB n.v.);

West Sulawesi. S. Kona-kona, Ds. Sondang, Kec. Kaluku Kab, 6 ii 1993, *Afriastini* 2053 (BO, K, L);

South East Sulawesi North Kolaka District, Rante Angin subdistrict, Tinukari village, 2 viii 2009, *Hidayat, Santika & Hapid* AH4095 (BO, E); Tinukari village, 4 viii 2009, *Potter, Sujadi, Shaputri, Asuar & Sarpin* 090804-01 (BO, E); Tinukari village, 29 vi 2011, *Widjaja, Sujadi, Santoso & Hapid* EAW9694 (BO, E);

Sulawesi. *de Vriese* 2 (L0277486 and L0277488) (L); *de Vriese & Teijsmann* 2 (L0277487) (L); *Unknown collector* 202 (L0277489) (L).

Sulawesi Group: 7 (Atkins et al., Chapter 3).

Notes *Cyrtandra celebica* is one of the most common and widespread species on Sulawesi. It is also one of the most striking and, allthough it is variable in terms of leaf shape and venation, it is easily recognised by its cauliflorous inflorescences and bright red corolla.

Blume (1826) originally described two species; *C. coccinea* from Java and *C. celebica* from Sulawesi. Clarke later reduced *C. celebica* to a variety of *C. coccinea* and listed two de Vriese collections from Sulawesi as examplar specimens (Clarke, 1883). Although the morphological similarities between the Javan and Sulawesi taxa are striking, there are differences between them. The difference originally highlighted by Blume is in the structure of the inflorescence, with those of the Javan species being sub-umbellate and those of Sulawesi being branched panicles (Blume, 1826). Clarke, when reducing the species to varietal level, also separated them on the indumentum of the young growth, the Sulawesi specimens being more densely hairy when young (Clarke, 1883). In addition to these differences, the corollas of the Javan taxa, although usually red, can be quite pale and even yellowish-white and the corolla lobes are larger and not as strongly recurved as in the Sulawesi species. Molecular phylogenetic research on the genus, has confirmed that *C. coccinea* from Java and Sulawesi are not con-specific and, in fact, the Javan material is more closely related to *C. floccosa* and *C. hispidula* than to *C. celebica* (Atkins et al., 2020). Here the Sulawesi material is treated as a distinct species, *C. celebica,* as Blume originally proposed.

Cyrtandra rhizantha was described by Kraenzlin (Kraenzlin, 1906) from a collection from Minahasa in Sulawesi and is treated for the first time as a synonym of *C. celebica*. The name *Cyrtandra rhizantha* was subsequently used illegitmately by Schlechter for a completely unrelated white flowered species from New Guinea (Schlechter, 1923).

Blume did not list any specimens when he described *C. celebica* and the only specimen that was collected early enough to have been seen by him is *Reinwardt* 1541 which is designated here as the lectotype.

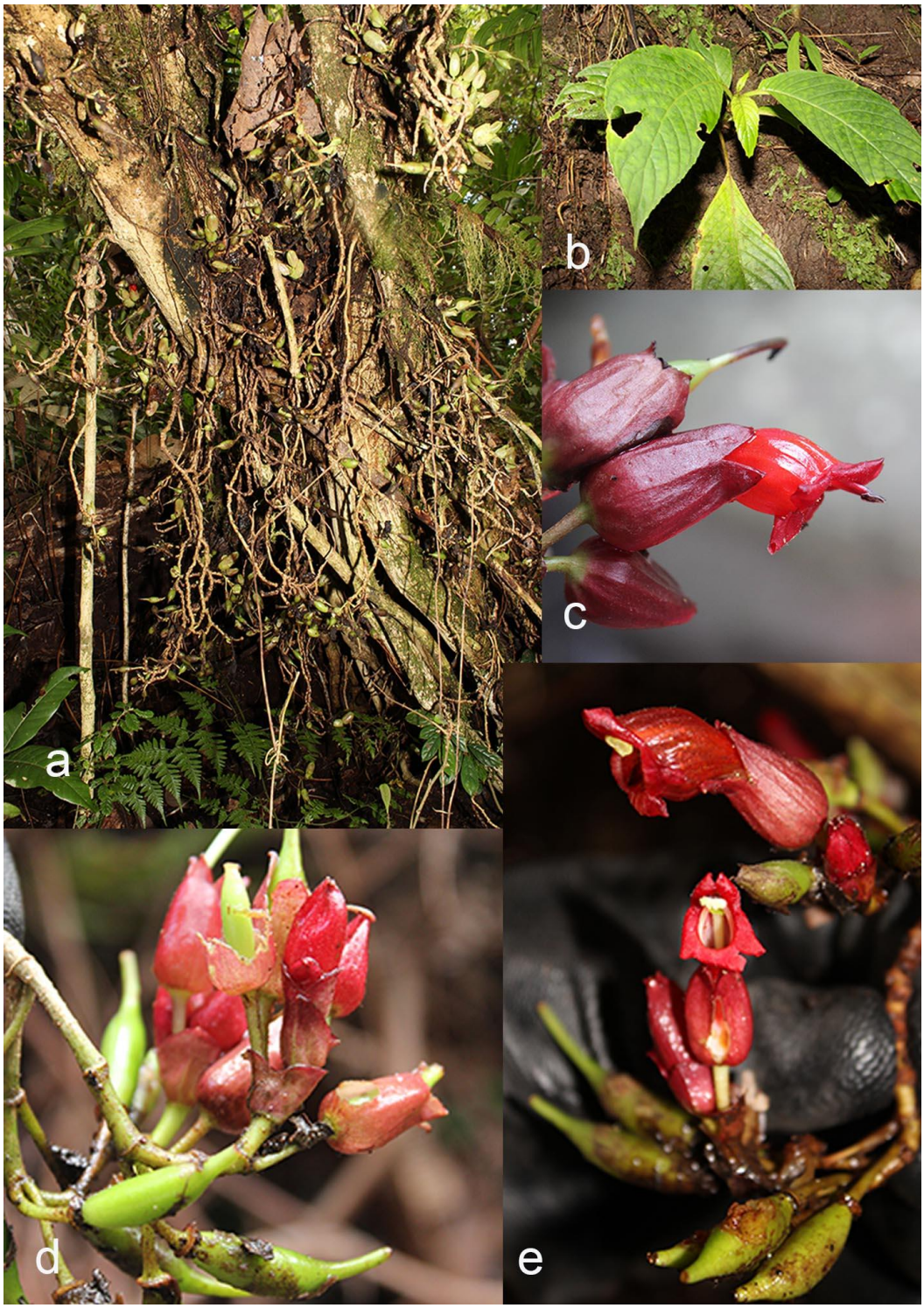


Fig. 2.16 Plate of *Cyrtandra celebica* showing a. habit b. leaves c. side view of flower d. infrutescence e. front and side view of flowers. Photos: Sadie Barber a. b BAKK8; c BAKK 15; d&e. BAKK12.

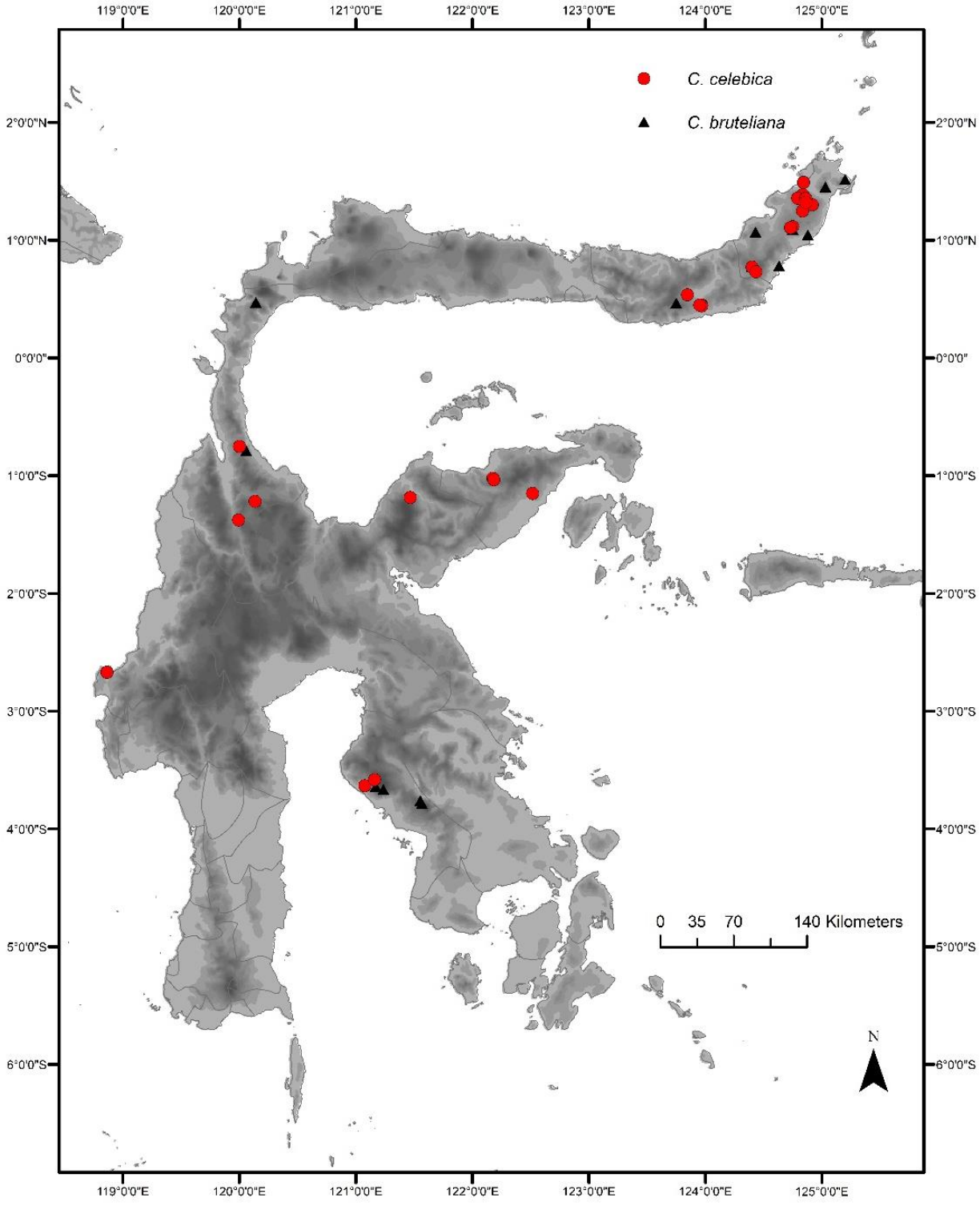


Fig. 2.17 Distribution of *Cyrtandra bruteliana* (black triangles) and *C. celebica* (red circles).

Cyrtandra engleri Koord., Meded's Land. Plantent. 19: 628 (1898). – Type: Celebes [Sulawesi], Minahassa, Lokon, 7 i 1895, *Koorders* 17204 (lectotype BO hic desig.; isolectotype L.).

Shrub or small tree to 4 m in height. ***Stems*** striate, hairy, densely so on young growth. ***Leaves*** opposite; one leaf of a pair markedly reduced or appearing alternate; petioles 6–10 mm long, densely hairy; blades of larger leaves 4.5–11 cm × 1.5–3 cm, oblanceolate to narrow-oblong, acuminate at apex, acumen 2–5 mm long, acute at base, not decurrent, slightly asymmetrical, margins subentire to minutely serrulate; 4–5 pairs of lateral veins, curving upwards and eventually running out to margin, tertiary venation reticulate, sub-glabrous above, sparsely hairy below, more densely so on midrib, veins and margin. *Reduced leaves* (where present) sessile, 2–3 mm long, cordate. ***Inflorescences*** axillary, sessile, 1–2-flowered; bracts 2–3 mm × 1mm, linear to narrow ovate, hairy; pedicels up to 5 mm long, densely hairy. ***Calyx*** evenly 5-lobed or occasionally appearing 4-lobed where two lobes are adpressed, whitish, flushed purple below, 10–13 mm long, lobes narrow, acuminate, 5–7 mm long, densely brown-hairy. ***Corolla*** white, sometimes with purple markings in throat, 15–20 mm long, narrow in basal half, widening gradually to mouth in apical half, upper lobes rounded 3 mm × 2mm, lower and lateral lobes 4 mm × 3 mm, densely hairy externally. ***Stamens*** with filaments 3–4 mm long, attached 7–8 mm from base of corolla, filaments glabrous; anthers 1 mm long, connected at tips before dehiscence, some glandular hairs on back of anthers; staminodes 3, 1 mm long, occasionally with a distinctive tuft of hairs at apex. ***Gynoecium*** 9–11 mm long; disc cupular with lobed, sparsely fringed margin, 1.5–2 mm long, glabrous; ovary and style densely eglandular hairy; stigma capitate, slightly bilobed, 1 mm across. ***Fruits*** oblong to narrow ovoid, 10–11 mm × 4 mm, densely hairy, base of style persistent, calyx not persistent.

Distribution: North Sulawesi and Gorontalo (Fig. 2.20).

Habitat and ecology. Hill and upland forest at an altitude of 600–1400 m.

Etymology. This species is presumed to be named after H.G.A. Engler, a German botanist, and contemporary of Koorders.

Proposed IUCN conservation category. This species has an EOO of 6412 km^2 and an AOO of 20 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). All of the collections are between 600 and 1400m which includes some of the most threatened forest types on the island (Cannon et al., 2007) and only one collection falls within a protected area (Gunung Lokon Nature Reserve) (UNEP-WCMC & IUCN, 2019). The species has not been re-collected since 1956 despite this being one of the better collected areas in Sulawesi. Due to its restricted distribution, the known threat to this habitat type and the lack of protection, it is considered to be Vulnerable under criteria VUD2.

Additional specimens examined: **North Sulawesi:** Minahasa, Mount Mahawae, 21 vi 1956 *Forman* 185 (BO, K, L, SING); Mount Mahawae, Tomohon, 23 vi 1956 *Forman* 224 (BO, K, L, SING); Tetepangan, Mount Lokon, 3 vii 1956, *Forman* 366 (BO, K, L); Bolaang Mongdonow, viii 1917, *Kaudern* 186 (L, S);
Gorontalo: Gunung Boliohutu, 24 iv 2002, *Atkins* et al. 209 (BO, E, L); Gorontalo, Gunung Boliohutu, 24 iv 2002, *Atkins* et al. 202 (E).

Sulawesi Group: 14 (Atkins et al., Chapter 3).

Notes. Cyrtandra engleri is part of a group of seven species on the island which share the characteristics of strongly anisophyllous leaves where the smaller leaf is highly reduced; white or yellow corollas and densely hairy calyces, corollas and fruits. The others in the group are *Cyrtandra gambutensis, C. gorontaloensis, C. balgooyi, C. widjajae, C. parvicalyx* and *C. sopuensis.*

Cyrtandra engleri is most similar to *C. widjajae,* a species originally described from South East Sulawesi (Kartonegoro & Potter, 2015) but which also extends in to North Sulawesi. *Cyrtandra engleri* can be distinguished from *C. widjajae* most easily by the smaller number of lateral vein pairs (4-5 in *C. engleri* vs 8-10 in C. widjajae) and the short-acuminate leaf apices (2-5 mm long in *C. engleri* vs up to 20 mm long in *C. widjajae*). *Cyrtandra engleri* also has a much denser, coarse indumentum, larger corollas, 15-20 mm long, as opposed to 11-15 mm long, often with tufted staminodes and with dense eglandular hairs throughout the length of the the style as opposed to a transition to glandular hairs at the top of the style near the stigma in *C. widjajae.* Corolla colour is noted in *C. engleri* as having purple markings in the throat, but the flowers of *C. widjajae* are

completely white. Two collections from Gunung Boliohutu in Gorontalo Province, some distance from the other collections in North Sulawesi, are included here although the leaf shape is somewhat different and the corollas lack the purple markings. Further collections are required to clarify the status of these specimens.

Koorders 17204 is selected here as the lectotype because it was originally annotated with the name *C. engleri* by Koorders*,* and is morphologically typical of this species.

Cyrtandra fasciata H.J.Atkins, Edinburgh J. Bot. 60(3): 309 (2004). – Type: Sulawesi, Gorontalo, Gunung Gambuta, 10 iv 2002, *Atkins* et al. 54 (holotype BO, isotype CEB, E, K, L).

Herb to 80 cm in height. ***Stems*** woody at base, bark tesselate, scaly, glabrous. ***Leaves*** opposite; both in each pair well developed but somewhat unequal in size; petioles 1–1.5 cm long, glabrous to sparsely hairy; blades 14–22 × 3.5-4.5 cm, narrow-elliptic to oblong, short acuminate at apex, base decurrent, margin serrulate; 9–12 pairs of lateral veins and some short side veins running to adjacent teeth, subglabrous above and below with some hairs on midrib and veins below. ***Inflorescences*** axillary, subsessile, 1–3-flowered; bracts brown or light green, c. 20 × 2 mm, linear, apex acuminate, sparsely felted-hairy, not connate; pedicels 4-5 mm long, sparsely hairy. ***Calyx*** tubular, longitudinally ridged, flushed reddish-pink at base, yellow above or pale yellow throughout, 28 mm long, three upper lobes c. 7 mm, acuminate, two lower lobes united in a shallowly notched limb c. 14 mm long, sparsely hairy. ***Corolla*** yellow with red stripes on lobes or pale yellow throughout, 32-40 mm long, erect, arcuate, narrow below, widening towards mouth, lobes strongly recurved, constricted just below rounded apex, all lobes 10 × 5–6 mm, sparsely hairy externally, densely glandular hairy internally, on lobes. ***Stamens*** with filaments 10 mm long, attached 18 mm above base of corolla, yellow; anthers 4 mm long, not cohering at tips before anthesis on specimens seen, back of anthers glandular hairy; staminodes c. 3 mm long. ***Gynoecium*** 20-25 mm long; disc cupular, margin even, glabrous, 1mm long; ovary glabrous; style glandular-hairy for whole length; stigma bilobed, lobes vertical, 1 mm long, densely glandular hairy on outer surface of lobes. ***Fruits*** ovoid, glabrous, green when unripe, 20 x 10 mm, calyx and base of style persistent.

Distribution: Gorontalo and Central Sulawesi (Fig. 2.20).

Habitat and ecology: Upland and montane forest at an altitude of 1000–1800m.

Etymology. This species is named for its distinctive striped corolla (Atkins, 2004).

Proposed IUCN conservation category. Based on the collections of fertile material of *C. fasciata* which can be identified with confidence, the EOO of this species is 8792 km^2 and the AOO is 12 km^2 using a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). The type collection is from Gunung Gambuta in the Bogani Nani Wartabone National Park and the others are from the Gunung Sojol and Gunung Dako Nature Reserves (UNEP-WCMC & IUCN, 2019). They are from relatively high altitudes in upland and montane forest which are the least threatened forest types in Sulawesi (Cannon et al., 2007). Due to the relative lack of threat and the protected areas in which the species grows a category of Least Concern is suggested for this species.

Additional specimens examined: **Central Sulawesi**. Mt Sojol, 26 ii 2000, *Mendum, Argent & Hendrian* 00160 (BO, E); ibid, 27 ii 2000, *Mendum, Argent & Hendrian* 00198 (BO, CEB, E, L); Gunung Galang-Dako, 13 vii 2018, *Wahyudi Santoso & Rusdi* WS324 (BO); Danau Tambing, 1700 m, 23 v 1979, *van Balgooy* 3442 (BO, E, L); Danau Kalimpa'a (Danau Tambing), 21 iii 2001, *Kessler* PK3060 (K, L);

South Sulawesi. Mamasa-Tabang, KBT. Polewali, 21 vi 1974, *Shuji Yoshida* 1234 (BO);

South East Sulawesi. Tinukari, on the way to camp 3, 30 vi 2011, *Widjaja* et al. 9711 (BO, E).

Sulawesi Group: 8 (Atkins et al., Chapter 3).

Notes Cyrtandra fasciata is similar vegetatively to *C. kinhoi, C. longistamina* and *C. flavomaculata* in having decurrent leaves and tesselate stems. It can be distinguished from these, however, by its erect flowers with striped corolla lobes constricted below the tips. It also has smaller leaves and much narrower inflorescence bracts than *C. kinhoi* and shorter pedicels and a much more tubular, ridged calyx than *C. longistamina.*

Two sterile collections from South and South East Sulawesi (*Yoshida* 1234 and *Widjaja* 9711) and two from Lore Lindu National Park in Central Sulawesi (*van Balgooy* 3442 and *Kessler* PK3060) have been placed here as they look most similar vegetatively to *C. fasciata* but there is, unfortunately, no flowering specimens available for study

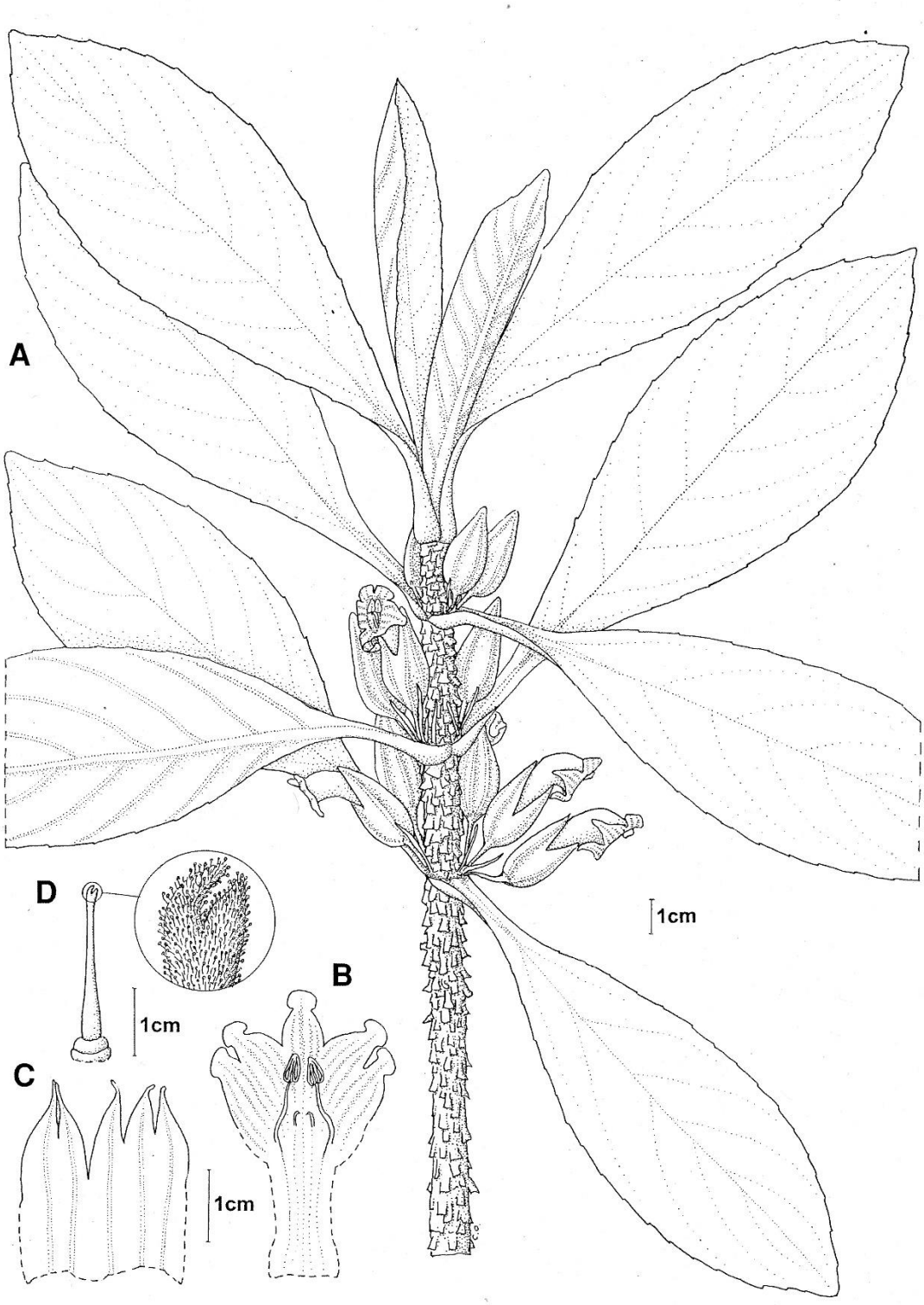


Fig. 2.18 Line illustration of *Cyrtandra fasciata* showing a. Habit b. Opened corolla showing position of stamens and staminodes c. Opened calyx showing inner surface d. Gynoecium including detail of stigma. Drawn by Christina Oliver from *Atkins* et al. 54. Reproduced from Atkins (2004).

Cyrtandra flavomaculata H.J.Atkins & Karton. **sp. nov.** ined.

Similar to *C. kinhoii* in its tessellate stems and decurrent leaves but differing in its corolla colour and indumentum (corolla white with distinctive yellow markings on lobes and glabrous externally in *C. flavomaculata* vs corolla white or flushed pink without markings and glandular hairy externally in *C. kinhoii*); and style indumentum (style densely glandular hairy in *C. flavomaculata* vs style glabrous, slightly eglandular hairy towards apex in *C. kinhoii*) - Type: Sulawesi, Lore Lindu NP, Tamping Lake vicinity, 4 viii 2018, *Ardi* WI299 (holotype KRB). **Fig. 2.19**

Herb** or **soft wooded shrub to 2m in height. ***Stems*** slightly tesselate and somewhat ridged. ***Leaves*** opposite, those of a pair subequal; petioles 1–2 cm long, sparsely hairy, winged and flushed white or pink; blades 21–25 cm x 5–6 cm, narrow oblong to narrow elliptic; apex short acuminate, base decurrent (appearing less so on older leaves as decurrent wing falls away), margin subentire towards the base, becoming serrate towards the apex; 11-18 pairs of lateral veins, looping up and running out to margin, tertiary venation reticulate, somewhat obscure; sparsely hairy above, more or less glabrous below with some hairs on the midrib and veins (more dense on young growth). ***Inflorescences*** axillary, often towards the base of the stem, subsessile, four to many-flowered, flowers at various stages of development; peduncle 5 mm long, glabrous; bracts narrowly obovate, with a slightly serrate margin towards the apex, off-white to light green, 25–40 mm x 7–9 mm, glabrous, quite leathery; apex long-acuminate; pedicels 5 mm long, glabrous. ***Calyx*** tubular, 23 mm long, light green or reddish, somewhat warty on some specimens, more or less glabrous, appearing 4-lobed as two of the lobes are divided only very briefly at the apex, lobes triangular, long-acuminate, 15 mm long. ***Corolla*** white with distinctive yellow marks on lower, and occasionally also upper lobes, 42mm long, funnel-shaped, narrow in basal half, then widening abruptly to mouth, more or less glabrous externally, lobes rounded, upper lobes 5 mm x 8 mm; lower and lateral lobes 8–10 mm x 8–10 mm; glandular hairy internally on lobes and in the tube below the anthers. ***Stamens*** with filaments 9 mm long, attached c. 20 mm from base of corolla, glabrous except for a few glandular hairs near the anthers; anthers 3.5 mm long, with a few glandular hairs, cohering at tips but not face to face before dehiscence; staminodes 3, laterals 4 mm long, central one highly reduced, less than 1 mm long. ***Gynoecium*** 30–35 mm long; disc cupular with a slightly undulate margin, glabrous, 3mm long; ovary glabrous, style densely glandular hairy; stigma bilobed, lobes 2.5–3 mm long. ***Fruits*** oblong, glabrous, c. 20 mm x 6 mm, green, base of style and calyx not persistent.

Distribution. Central, South, South East and West Sulawesi (Fig. 2.20).

Habitat and ecology. Hill, upland and montane forest, sometimes in disturbed areas at an altitude of 500-1750 m. One specimen (*Hennipman* 5939) records that it was collected from a limestone area.

Etymology. This species is named for its distinctive yellow colouring on the lower, and occasionally also upper, corolla lobes.

Proposed IUCN conservation category. The EOO of this species is 17,578 km^2 and the AOO is 28 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). Some of the collections fall within the protected area of the Lore Lindu National Park (UNEP-WCMC & IUCN, 2019) but most are in areas without any formal protection. The species has quite a wide altitudinal range but many of the collections are from the more threatened hill forest zone (Cannon et al., 2007). Due to the low number of collections, relative lack of protection and known threat to this habitat this species is considered to be Vulnerable under VUD2.

Additional specimens examined. **Central Sulawesi.** Track to shelter 2, Mt. Nokilalaki, 24.vii.18, *Ardi* WI229 (KRB); Road to Lake Lindu, c.60km SSE of Palu, 30 v 1979, *van Balgooy* 3565 (A, BO, E, L); Road to Lake Lindu, c.60km SSE of Palu, 30 v 1979, *van Balgooy* 3571 (A, BO, E, L);

South Sulawesi. Gunung Pere, south of Soroako, 20 vi 1979, *Hennipman* 5939 (A, BO, E, L);

South East Sulawesi. North Konawe, Linomoyo Transmigration Village, 16 ii 2017, *Ardi* WI164 (KRB); Kolaka, along the trail to Gunung Mekkongga, 18 iii 2006, *Girmansyah* 580 (BO).

Fig. 2.19 Plate of *Cyrtandra flavomaculata* showing a. habit b. bracts c. fruits d. side view of corolla e. front view of corolla. Photos: Wisnu Ardi [WI299].

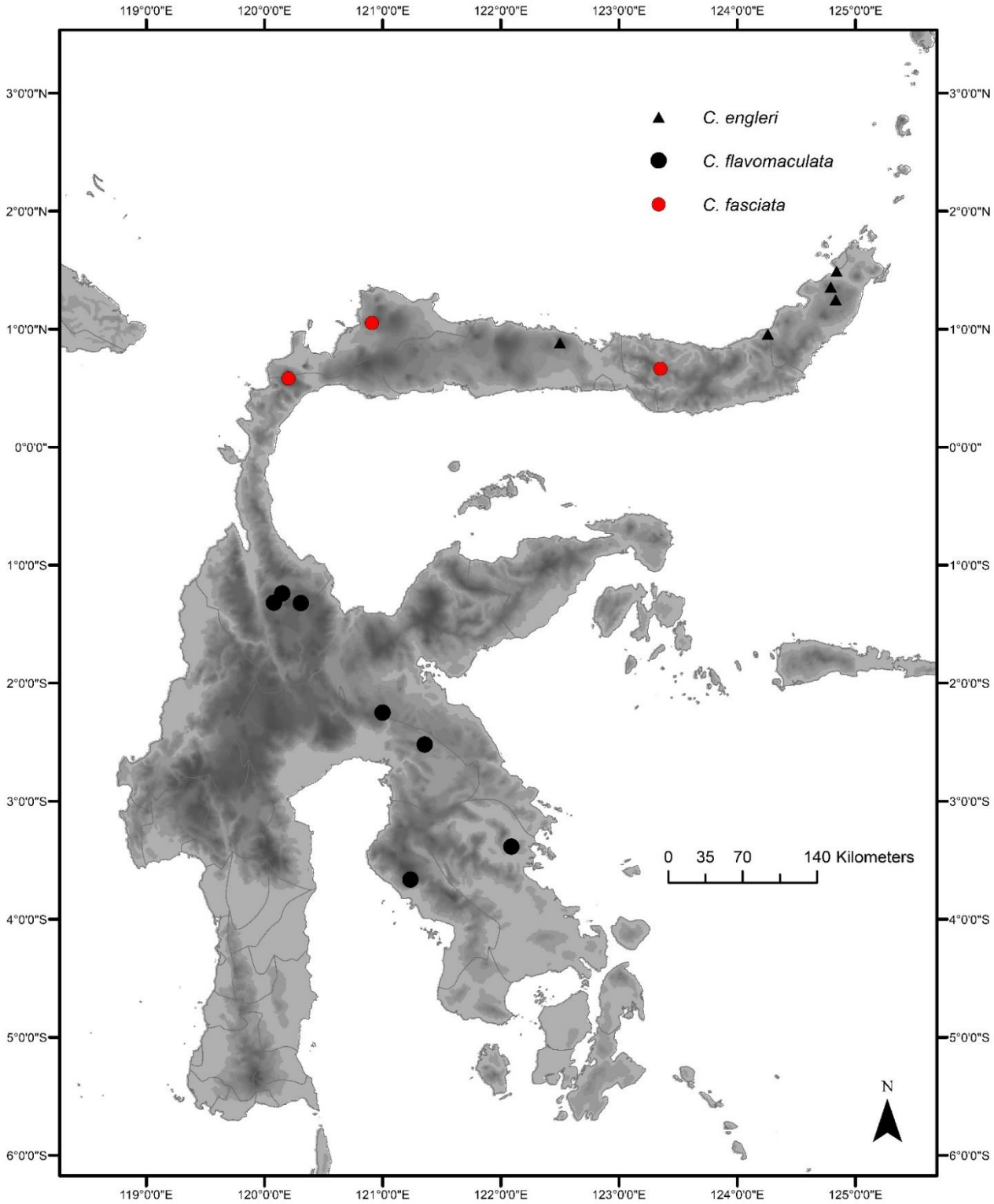


Fig. 2.20 Distribution of *Cyrtandra engleri* (black triangles)*, C. fasciata* (red circles) and *C. flavomaculata* (black circles).

Sulawesi Group: 8 (Atkins et al., Chapter 3).

Notes. This species is most similar vegetatively to *Cyrtandra kinhoii, C. fasciata* and *C. longistamina* in having decurrent leaves and tesselate stems. It can be distinguished from *C. fasciata* most easily by its wider, obovate inflorescence bracts 7–9 mm wide as opposed to linear bracts that are 2 mm wide and and from *C. longistamina* by its oblong fruits on short pedicels up to 5 mm long as opposed to sub-globose fruits on long pedicels up to 30 mm long. Some of the collections now included in this species were originally cited under *C. kinhoii* (Kartonegoro et al., 2018). With better material of *C. flavomaculata,* however, it is clear to see that there are differences in the corolla and style in terms of colouring and indumentum as detailed in the diagnosis. The base of the leaves also have a distinctive white or purplish tinge and a somewhat different papery texture to the rest of the leaf that is not seen in *C. kinhoii*. These papery bases are sometimes lost as the leaves get older so that they appear less decurrent. The two species are also geographically separated with *C. kinhoii* restricted to North Sulawesi and *C. flavomaculata* distributed in Central, South and South East Sulawesi.

According to notes on *Hennipman* 5939, the young leaves are used for the preparation of fish soup (sajor ikan).

Cyrtandra floccosa R.Bone & H.J.Atkins, Edinburgh J. Bot. 70(3): 457 (2013). – Type: Sulawesi, Mt Rantemario, 26 iv 2009, *Thomas & Ardi* 09-90 (holotype E; isotypes BO, L). **Fig. 2.21**

Shrub or tree 2−4 m in height. ***Stems*** strongly fenestrated, often with conspicuous swollen nodes, glabrescent, densely hairy when young. ***Leaves*** opposite, those of a pair more or less equal, often clustered at tips of branches; petioles 12–25 mm long, hairy; blades 6.5–13 × 3–6 cm, elliptic to ovate, apex acute, base acute or rounded, somewhat coriaceous, drying dark brown or black, margin crenate to serrate; 7-9 pairs of lateral veins, looping upwards and running out to margin, tertiary venation reticulate; sparsely hairy above, hairy below densely so on mid rib and veins. ***Inflorescences*** axillary, pedunculate, 1–2-flowered; peduncles c. 6–11 mm long; bracts 3–5(−7) mm long, triangular to ligulate, leafy (with mid-rib); pedicels 7–20 mm, densely hairy. ***Calyx*** tubular, green-brown,

coriaceous, 19–34 mm long, two lower lobes 8–16 mm long, acuminate at apex, three upper lobes divided briefly at apex, densely hairy externally. ***Corolla*** light yellow, 26–45 mm long , tube narrow at base, widening and becoming slightly pouched at c. 1/3 of length; lobes reflexed, two small dorsal lobes c. 5 mm long, two large lateral lobes c. 12 mm long, 1 ventral lobe c. 7 mm long, hairy to glabrescent externally, becoming sparsely hairy distally at ends of lobes, glabrous internally at base becoming glandular-hairy distally. ***Stamens*** with filaments 9–10 mm long, attached c. 20 mm from base of corolla tube; anthers 3–4 mm long, cohering at tips before and during dehiscence; staminodes 3, lateral staminodes c. 3 mm long, central staminode highly reduced, less than 1 mm long. ***Gynoecium*** c. 29 mm long; disc cupular with shallowly lobed margin, c. 4 mm long; ovary glabrous; style sparsely glandular hairy at base, becoming dense towards the apex; stigma peltate, c. 3 mm wide, surface densely papillose; stigma and stamens visible beyond corolla mouth. ***Fruits*** ovoid, green, drying black, 15–25 mm × 6–8 mm, glabrous; calyx usually not persistent in fruit, base of style persistent.

Distribution. South Sulawesi: Latimojong Mountains (Fig. 2.24).

Habitat and ecology. Tropalpine forest at an altitude of 2800-3000m.

Etymology. The specific epithet refers to the floccose indumentum which is particularly dense on juvenile leaves and shoots (Bone & Atkins, 2003).

Proposed IUCN conservation category. The EOO of this species is 7 km^2 and the AOO is 12 km^2 based on 2 × 2 km grid cell size) under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). The species occurs in Tropalpine vegetation over 2800 m altitude in and around the western boundary of the Pegunungan Latimojong Protection Forest. As this habitat type is in good condition and not considered at risk (Cannon *et al.*, 2007), it is considered unlikely that this species is in decline. It has been collected on three different botanical expeditions in the Latimojong Mountains, most recently in 2009. Following Bone & Atkins (2013), this species is considered to be of Least Concern.

Additional specimens examined. **South Sulawesi**: B. Rante Mario, 3000 m, 1929, *Kjellberg* 4046 (BO, S); Latimojong Mts south of Ninimori, 2950 m, 23 x 1969, *Sands* 296 (BO, E, K); ibid., *Sands* 344 (E, K); Gunung Rantemario, 2788 m, 26 iv 2009, *Thomas & Ardi* 09-89 (E, BO, L).

Sulawesi Group: 9 (Atkins et al., Chapter 3).

Notes. This species is very distinctive in Sulawesi, characterised by its rusty, floccose indumentum throughout and large pale yellow flowers.

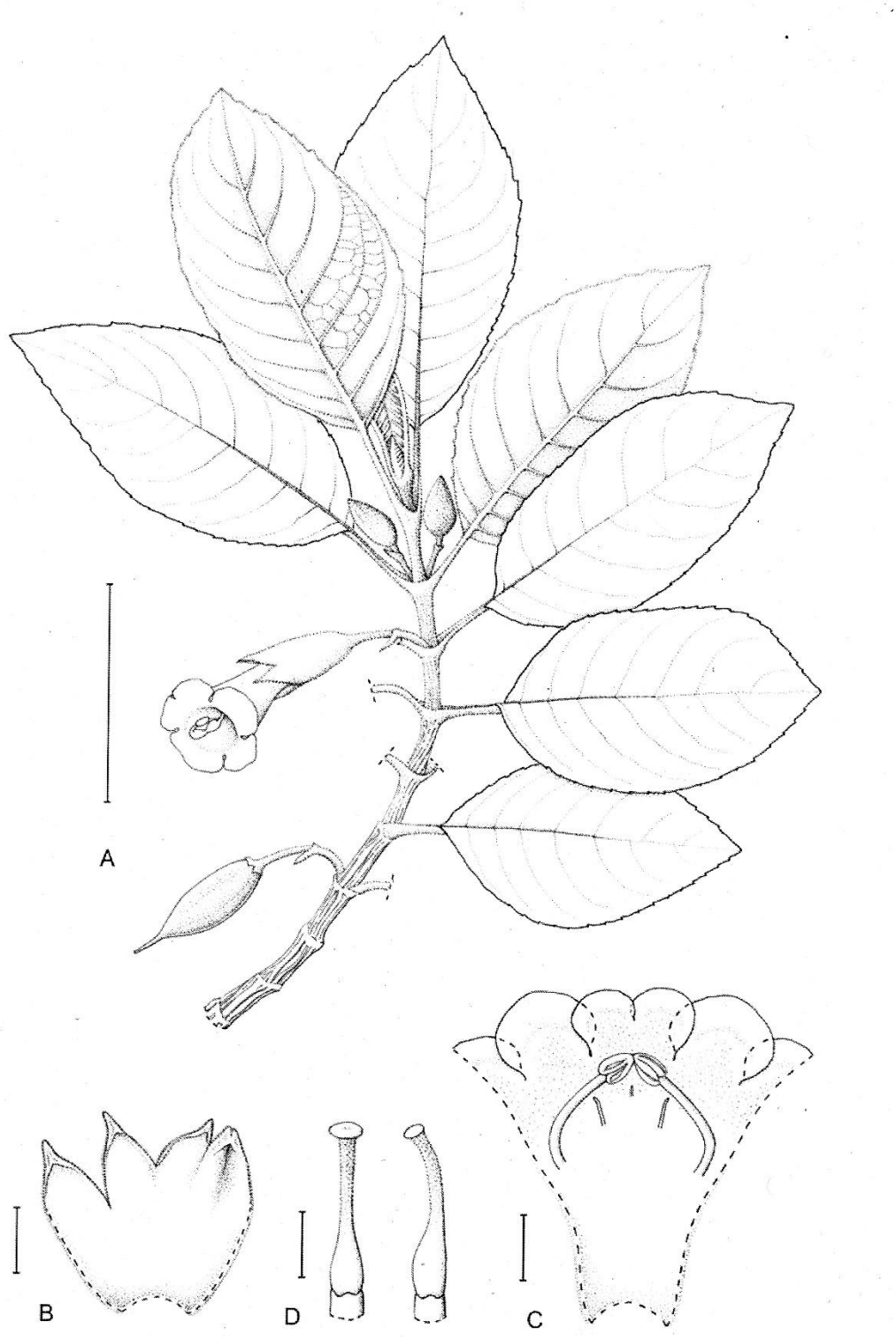


Fig. 2.21 Line illustration of *Cyrtandra floccosa* showing a. Habit b. Opened calyx showing inner surface c. Opened corolla showing position of stamens and staminodes d. Gynoecium and disc. Drawn by Claire Banks from *Thomas & Ardi* 09-90. Reproduced from Bone & Atkins (2013).

Cyrtandra gambutensis Karton. & H.J. Atkins, Edinburgh J. Bot. 75(2): 180 (2018). – Type: Sulawesi, Gorontalo Province, Mt Gambuta, 8 iv 2002, *Atkins, Mendum, Newman, Hendrian & Sofyan* 38 (holotype E; isotypes BO, CEB, K, L, SING). **Fig. 2.22**

Shrub 0.7–2.5 m in height. ***Stems*** striate, short hairy, appearing pubescent. ***Leaves*** opposite, unequal; one leaf of a pair markedly reduced; petioles 0.8–1.3 cm long, hairy; blades 6–9.5 × 1–2.5 cm, oblanceolate, apex short-acuminate, acumen 4–5 mm long, base attenuate, slightly asymmetrical, margins subentire; 8–11 pairs of lateral veins running straight out to margin, sparse tertiary venation, glabrous above, hairy below, most densely so on midrib, veins and margin; reduced leaves cordate, 5 × 4 mm, resembling the larger leaves in other respects. ***Inflorescences*** axillary, sessile, 2–3-flowered; bracts oblong-lanceolate, 5 × 1 mm, hairy on both sides; bracteoles lanceolate, hairy, 3–4 x 0.5 mm; pedicels 3–5 mm long, densely hairy. ***Calyx*** tubular, white, green in bud, c. 15 mm long, densely hairy externally, three upper lobes c. 7 mm long, acuminate, two lower lobes c. 8 mm long, triangular, acuminate at apex. ***Corolla*** white with purple markings on lobes, tube narrow in basal third, widening to mouth in apical two thirds, 19–20 mm long, densely hairy externally, upper lobes rounded, 4 × 2 mm, lower and lateral lobes ovate, 5 × 3 mm. ***Stamens*** with filaments 5 mm long, attached 8 mm above base of corolla, white; anthers 1 mm long, not coherent at apices, purple; staminodes 3, c. 2 mm long. ***Gynoecium*** c. 11 mm long; disc cupular with undulate, fringed margin, glabrous externally, 2 mm long; ovary and style densely eglandular hairy; stigma bilobed, 2 mm across. ***Fruits*** oblong, dark green, cylindrical, densely hairy, 9 × 3 mm; calyx not persistent, base of style persistent.

Distribution. North Sulawesi (Fig. 2.24).

Habitat and ecology. Hill and upland forest at an altitude of 520–950 m.

Etymology. Named after the mountain on which the type specimen was collected (Kartonegoro et al., 2018).

Proposed IUCN conservation category. The low number of collections for this species means that it has not been possible to calculate an EOO for this species but it has an AOO of 8 km^2 based on 2 × 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). The collections are from hill and upland forest which are threatened in Sulawesi (Cannon et al., 2007) but from within the boundaries of the Bogani Nani Wartabone National Park (UNEP-WCMC & IUCN, 2019). Following Kartonegoro et al. (2018) it is given a category of Vulnerable based on its restricted distribution and the known threat to lowland and lower montane forest in Sulawesi (Cannon et al., 2007).

Additional specimens examined. **North Sulawesi**: Bolaang Mongondow, Dumoga Bone National Park, G. Mogogonipa, 10 iv 1985, *de Vogel & Vermeulen* 7081 (L).

Sulawesi Group: 14 (Atkins et al., Chapter 3).

Notes. This species is part of a group in Sulawesi that share the characteristics of strongly anisophyllous leaves (wherein the smaller leaf is highly reduced); white or yellow corollas and densely hairy calyces, corollas and fruits. The other species in the group are *C. widjajae* Karton.*,* C. *gorontaloensis* H.J. Atkins and *C. engleri* Koord*. Cyrtandra gambutensis* can be distinguished from the others by its narrow leaves, sparse tertiary venation and numerous secondary veins which run straight out to the margin without looping upwards.

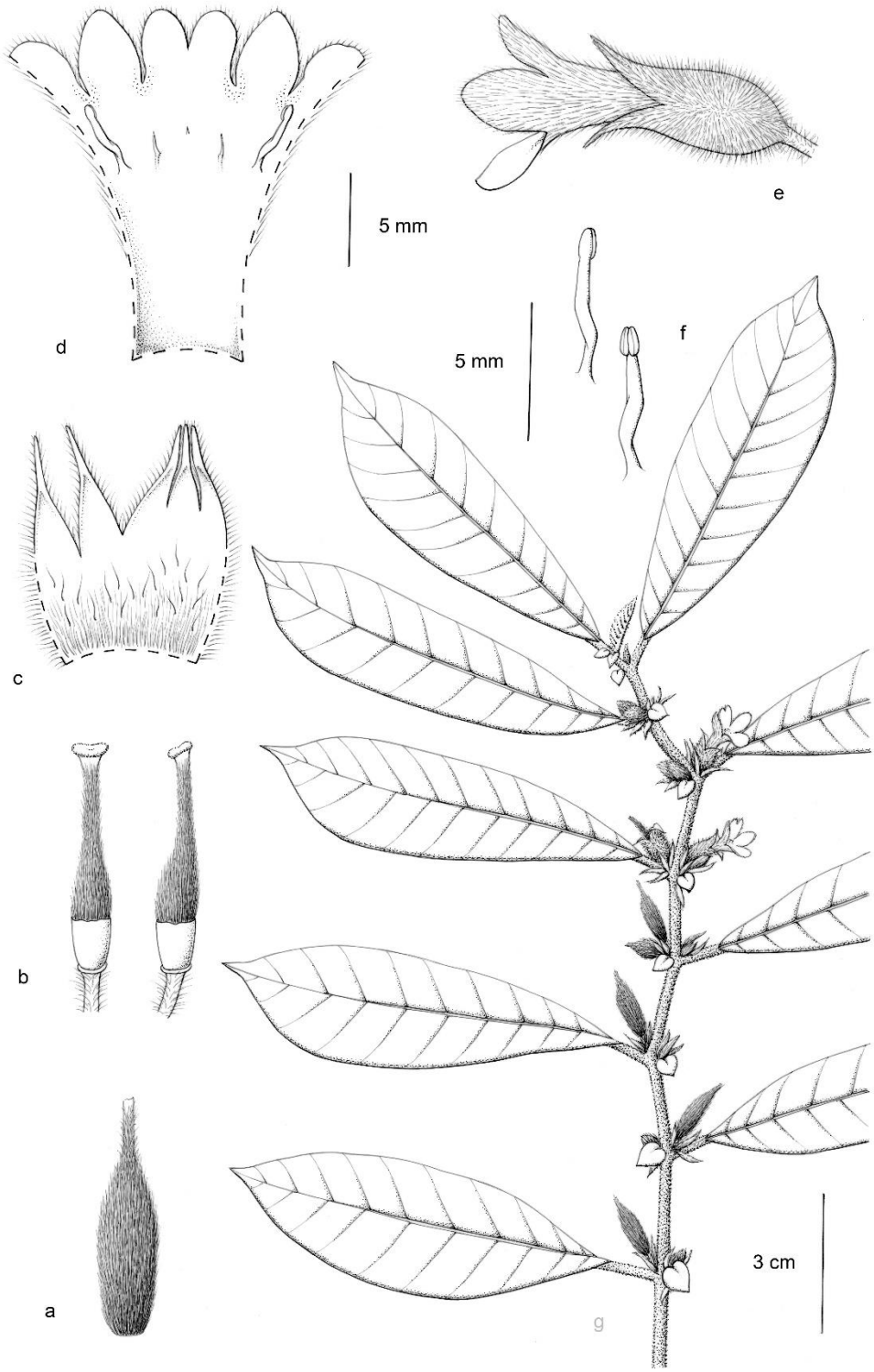


Fig. 2.22 Line illustration of *Cyrtandra gambutensis* showing a. Fruit b. Gynoecium showing disc and pedicel c. Opened calyx showing inner surface d. Opened corolla showing position of stamens and staminodes e. Side view of corolla f. Stamens and anthers g. Habit. Drawn by Claire Banks from *Atkins* et al. 38. Reproduced from Kartonegoro et al. (2018).

Cyrtandra geocarpa Koord., Meded.'s Land. Plantent. 19: 627 (1898). – Type: Celebes [Sulawesi], Minahassa, Gunung Lolomboelan, 15 iv 1895, *Koorders* 19377 (lectotype BO hic desig.). **Fig. 2.23**

Branching herb or ***shrub*** to 1m in height. ***Stems*** striate, glabrous, hairy on young growth. ***Leaves*** opposite; those of a pair well developed but somewhat unequal in size; petiole 10–15 mm long, sparsely hairy to hairy; blades 8–16(–24) cm × 2–8(–10) cm, narrow oblong to oblanceolate, apex acuminate, base acute, not decurrent, more or less symmetrical; margin serrulate to lobed; 5–7 pairs of lateral veins, curving upwards and running out to margin, subglabrous above, sparsely hairy below, more densely so on midrib and veins. ***Inflorescences*** on trailing, rooting stems from base of main plant; trailing stem c.1 mm in diameter, up to 50 cm long, glabrous; bracts 1–2 mm × 1 mm, linear to linear-lanceolate, hairy, not connate. ***Calyx*** green to reddish-brown, 9–12 mm long, five-lobed, lobes subulate to linear, acuminate at apex, 3–8 mm long, hairy externally. ***Corolla*** white, sometimes with pale purple internally on lobes and yellow guidemarks in throat, 25–40 mm long, very narrow in basal half then widening to mouth, lobes spreading not strongly recurved, upper lobes c. 7 x 6 mm, lower and lateral lobes c. 9 x 8 mm, sparsely hairy externally, glandular hairs at base of lobes and on base of tube below filaments. ***Stamens*** with filaments 8–15 mm long, attached 12–20 mm from base of corolla, glabrous; anthers 1–2 mm long, cohering at apices and face to face before dehiscence; staminodes 3, 1.5-3 mm long. ***Gynoecium*** 15–20 mm long; disc cupular, 1.5-2 mm long, glabrous; ovary subglabrous; style sparsely eglandular and glandular hairy, more densely so towards apex; stigma appearing peltate or slightly bilobed, up to 2 mm across. ***Fruits*** oblong, brown-green, subglabrous, 15 mm × 5 mm, calyx and style persistent.

Distribution. Gorontalo, North Sulawesi, Central Sulawesi (Fig. 2.24).

Habitat and ecology. Lowland to upland forest at an altitude of 150–1500 m.

Etymology. The name of this species reflects the position of the flowers and fruits on long, trailing stems at the base of the plant.

Fig. 2.23 Plate of *Cyrtandra geocarpa* showing a. side view of flower b. front view of flower c. habit. Photos: Sadie Barber. *Barber* et al. BAKK 25

Proposed IUCN conservation category. The EOO of this species is 74,685 km^2 and the AOO is 56 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). It is found over a wide altitudinal range and from three of the island's provinces and has been collected on a number of recent expeditions (in 2000, 2002, 2008, 2016). Some of the collections fall within the boundaries of either the Lore Lindu National Park, Gunung Sojol Nature Reserve or the Bogani Nani Wartabone National Park (UNEP-WCMC & IUCN, 2019). Due to its distribution and level of protection in a number of areas, this species is considered to be of Least Concern.

Additional specimens examined: **North Sulawesi**. Gunung Lolombulan, 4 ii 2019, *Ardi* WI406 (KRB); Bolaang Mongondow Selatan, Tapakolintang area, 29 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK 7 (BO, E); Bolaang Mongondow, Mt London, 31 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK 25 (BO, E); 220 km W of Menado, 50 km inland from Pangi, 7 iii 1990, *Burley, Tukirin* et al. 3701 (A, K, L); Minahassa, 1895, *Koorders* 17180 (BO); Bolaang Mongondow, Dumoga Bone National Park, 14 iii 1985, *de Vogel & Vermeulen* 6527 (BO, L); Dumoga Bone National Park, 3 iv 1985, *de Vogel & Vermeulen* 6971 (BO L);
Gorontalo. Path from Bululi to Gunung Boliohutu, 22 iv 2002, *Scott* 02-99, grown at RBGE as accession 20021222A, vouchered as *Atkins* 12 (E); ibid, 22 iv 2002, *Atkins* et al. 139 (BO, CEB, E); Lombongo, 30 iv 2002, *Atkins* et al. 252 (BO, E);
Central Sulawesi. Area of Mt Nokilalaki, 2 iv 1975, *Meijer* 9451 (BO, L); Area of Mt Nokilalaki, along Sungai Pehoeia, 5 iv 1975, *Meijer* 9601 (BO, L); Area of Mt Nokilalaki, SE of Lake Lindu, 3 v 1975, *Meijer* 9971 (BO, L); Mt Sojol, 5 ii 2000, *Mendum* et al. 00149 (BO, E); Gunung Galang-Dako, 5 vii 2018, *Wahyudi Santoso Rusdi* WS186 (BO).

Sulawesi Group: 11 (Atkins et al., Chapter 3).

Notes. There are four species in Sulawesi with trailing inflorescences that originate at the base of the stem: *C. hypogaea, C. geocarpa, C. rantemarioensis* and *C. luteiflora. Cyrtandra geocarpa*, can be distinguished from these other geoflorous taxa by a combination of its slender (less than 1 mm diameter), unbranched inflorescence axis, cupular disc and large, white flowers.

One of the two specimens collected by Koorders and annotated with the name *C. geocarpa*, *Koorders* 19377, is designated here as the lectotype.

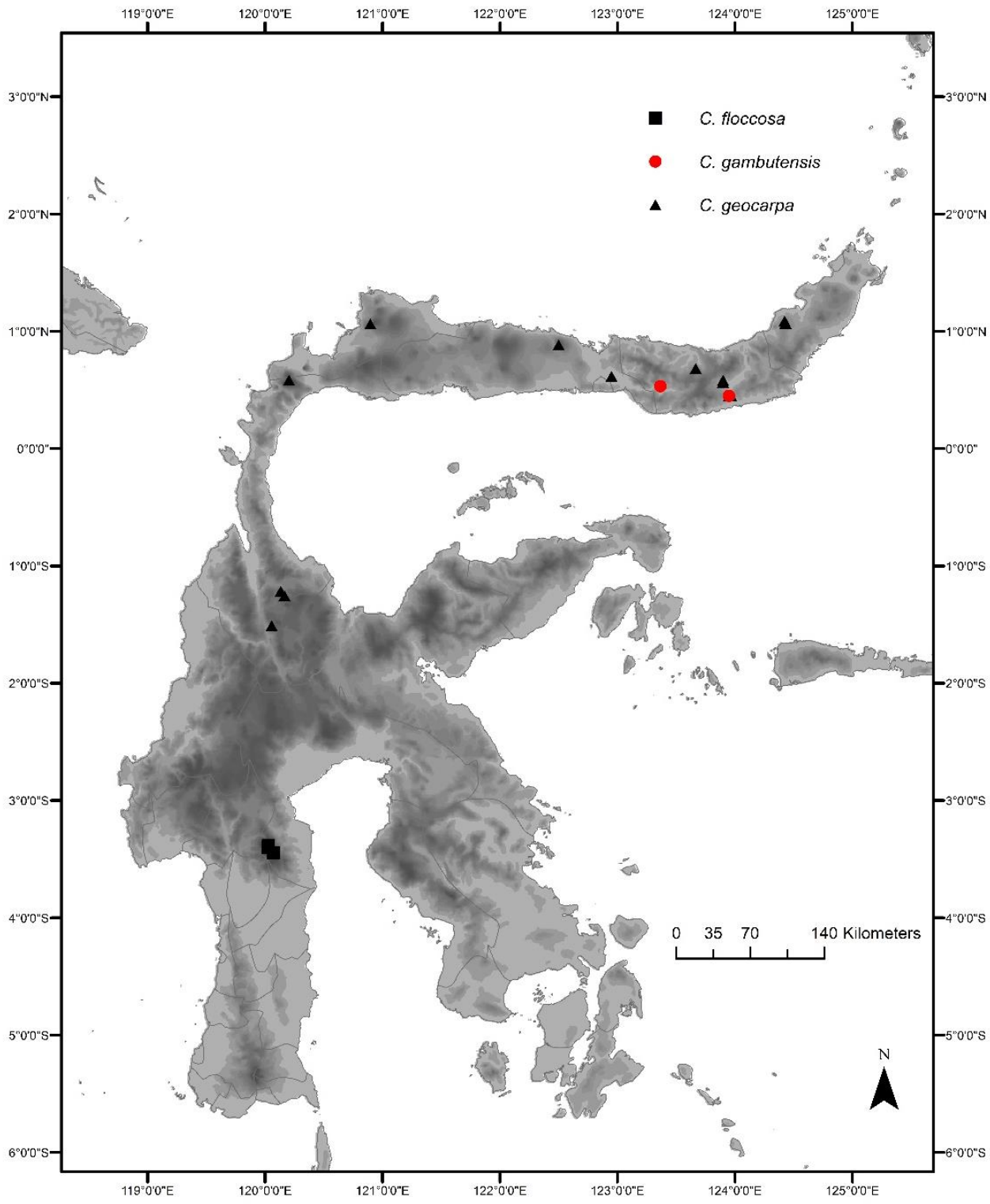


Fig. 2.24 Distribution of *Cyrtandra floccosa* (black squares), *C. gambutensis* (red circles) and *C. geocarpa* (black triangles).

Cyrtandra gorontaloensis H.J.Atkins, Edinburgh J. Bot. 60(3): 307 (2004). – Type: Sulawesi, Gorontalo, Gunung Gambuta, 12 iv 2002, *Atkins* et al. 91 (holotype BO, isotype E, L). **Fig. 2.25**

Branching shrub to 2 m in height. ***Stems*** striate, sparsely hairy, more densely so when young. ***Leaves*** appearing alternate, occasionally opposite with one of each pair vestigial and scale-like; petiole (5-)10–15 mm long, hairy; blade of developed leaf (4-)7–11.5 × 1.5–3.5 cm, narrowly oblong to oblanceolate, apex acuminate, base narrowly cuneate and slightly asymmetric, margin subentire; 4–5 pairs of lateral veins curving towards margin, occasionally branching, tertiary venation sparse, subglabrous above and below, sparsely hairy on midrib and veins and along margin. *Reduced leaves* (where present) 5 × 1 mm, scale-like. ***Inflorescences*** axillary, 1–2-flowered, subsessile; peduncles up to 3 mm long, hairy; bracts 1–1.5 mm long, narrowly ovate to linear; pedicels (5-)15–30 mm long, hairy. ***Calyx*** 7–10 mm long, pale green, 3 upper lobes united into a shallowly notched limb, 2 lower lobes similarly united, hairy externally. ***Corolla*** creamy white to pale yellow, 17–20 mm long, tube narrow below, gradually widening to mouth, lobes rounded, not recurved, upper lobes 4 mm x 4 mm, lower and lateral lobes slightly larger 5 × 5 mm, white-hairy externally. ***Stamens*** with filaments 3–4 mm long, attached 12 mm from base of corolla, glabrous, white; anthers 1.5 mm long, cohering at apices before dehiscence, brown; staminodes 3, 1 mm long. ***Gynoecium*** 8–16 mm long; disc unilateral, with a slightly lobed margin, 1–1.5 mm long, glabrous externally, hairy internally and with a fringe of hairs; ovary densely hairy; style densely hairy, glandular towards apex; stigma bilobed, 1 mm across. ***Fruits*** ovoid, green, 12–18 × 5–6 mm, hairy, calyx not persistent, base of style persistent.

Distribution. Gorontalo and North Sulawesi (Fig. 2.29).

Habitat and ecology. Upland forest at an altitude of 1300–1500 m

Etymology. This species is named after the northern Sulawesi province of Gorontalo from where the type specimen was collected (Atkins, 2004).

Proposed IUCN conservation category. The EOO of this species is 1,613 km^2 and the EOO is 16 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1).

One of the collections falls within the boundaries of the Bogani Nani Wartabone National Park, one just outside and two others within the Gunung Ambang Nature Reserve (UNEP-WCMC & IUCN, 2019) and, as such, should be provided with some level of protection. All of the collections are in upland forest between 1300 and 1500 m which is a less threatened habitat in Sulawesi than lowland areas (Cannon et al., 2007). This species is considered to be of Least Concern due to the level of protection and low perceived threat (Cannon et al., 2007).

Additional specimens examined: **North Sulawesi**. Bolaang Mongondow, Gunung Ambang Nature Reserve, 1337 m, 2 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK43 (BO, E); Paya-paya area of Gunung Ambang range, 4 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK68 (BO, E); Dumoga Bone National Park, Bolaang-Mongondow, vicinity of G. Sinombayuga, 1400m, 30 ix 1991, *Milliken* 1131 (L).

Sulawesi Group: 14 (Atkins et al., Chapter 3).

Notes. This species is part of a group in Sulawesi that share the characteristics of strongly anisophyllous leaves; white or yellow corollas and densely hairy calyces, corollas and fruits. This species is distinctive within this group by its combination of seemingly alternate leaves (and reduced scale-like rather than cordate leaves where present), sparse tertiary venation, unilateral disc and style with glandular hairs towards the apex. This species was first described from two collections in the Bogani Nani Wartabone National Park. Two recent collections from Gunung Ambang (*Barber* et al., BAKK43 and BAKK68) with slightly shorter pedicels than the type and occasionally two flowers per inflorescence have allowed the original description to be updated.

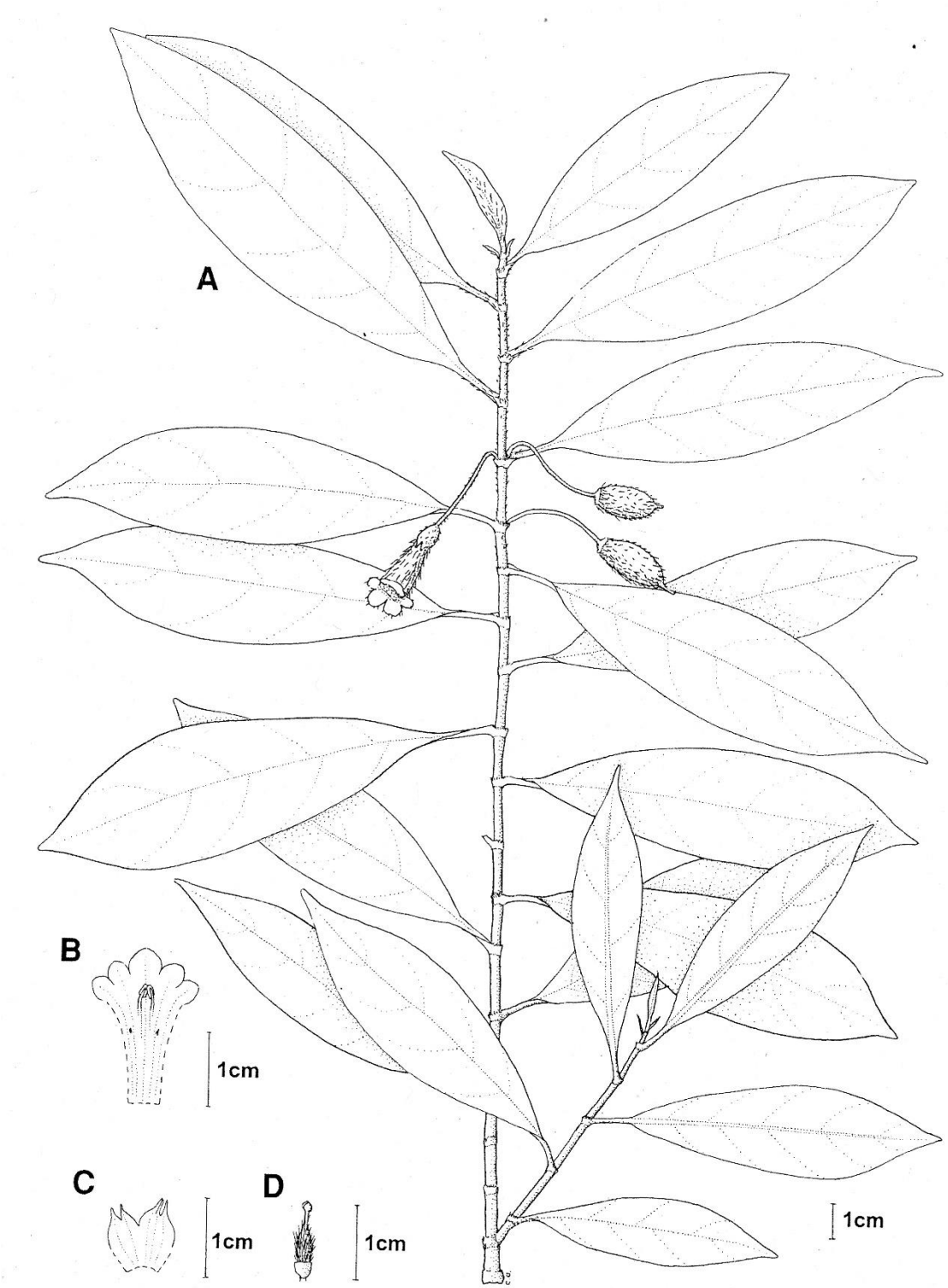


Fig. 2.25 Line illustration of *Cyrtandra gorontaloensis* showing a. Habit b. Opened corolla showing position of stamens and staminodes c. Opened calyx showing inner surface d. Gynoecium. Drawn by Christina Oliver from *Atkins* et al. 91 and *Milliken* 1131. Reproduced from Atkins (2004).

Cyrtandra hekensis Karton. & H.J.Atkins**,** Edinburgh J. Bot. 75(2): 182 (2018) – Type: Sulawesi, Mt Hek, 9 iv 2008, *Thomas & Ardi. 08-26* (holotype BO; isotype E). **Fig. 2.26**

Herb to 25 cm in height. ***Stems*** ridged, striate, upper stem appearing reddish, from dense, coarse indumentum on young growth, older stems glabrous. ***Leaves*** opposite, slightly unequal; those of a pair well developed but one slightly smaller; petioles 0.8–2 cm long, densely, coarse hairy on young growth becoming glabrous on older growth, narrowly winged; blades 7–7.5 x 1.6–3 cm (larger leaves), 3.5–5 x 1.3–1.7 cm (smaller leaves), narrow elliptic or oblong to somewhat oblanceolate, apex acuminate, base attenuate, margin serrate; 4–6 pairs of lateral veins and reticulate tertiary venation; dark green and mostly glabrous above with some hairs towards the base, paler green and with scattered hairs below with coarse hairs on the midrib and veins. ***Inflorescences*** axillary, subsessile to shortly pedunculate, 1–2 flowered; peduncles red, 2–3 mm long, hairy; bracts green, 9 x 5–6 mm, ovate, connate 4 mm from base, with some coarse hairs on midrib and margins, margin slightly serrate; bracteoles paired, green, 6–8 x 3 mm, oblong, with coarse hairs on midrib and margins; pedicels 2–3 mm long, glabrous. ***Calyx*** tubular, pale green, 10–11 mm long, upper lobes c. 2 mm long, lower lobes c. 3 mm long, acuminate, glabrous except for a few tufts of hair at apex. ***Corolla*** white with greenish yellow markings in throat, c. 15 mm long , tube narrow in lower third, widening to mouth in apical two thirds, hairy externally in the apical third, particularly densely so towards the mouth, upper lobes rounded, 3–4 x 3 mm, lower and lateral lobes rounded, 3 x 3 mm. ***Stamens*** with filaments c. 5 mm long, attached c. 6 mm from base of corolla, glabrous; anthers c. 1 mm long, coherent at apices; staminodes 2, c. 0.5 mm long. ***Gynoecium*** c.10 mm long; disc cupular with lobed margin, glabrous externally, c. 1.5 mm long; ovary glabrous, style eglandular hairy towards apex; stigma slightly bilobed, lobes small, c. 1 mm across. ***Fruits*** ovoid, glabrous, verrucose, drying light brown, 6 x 4 mm; base of style and calyx persistent, bracts sometimes persistent.

Distribution. Central Sulawesi: Luwuk (see Fig. 2.29).

Habitat and ecology. Hill forest at an altitude of 420–660 m.

Etymology. This species is named after the mountain on which it was collected.

Proposed IUCN conservation category. The low number of collections for this species means that it is not possible to calculate an EOO but it has an AOO of 4 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). This species is known only from Mt Hek, Luwuk Regency where it was collected at relatively low altitude during expeditions in 2004 and 2008. This forest type is one of the most threatened in Sulawesi (Cannon et al., 2007) and Mt Hek is in an area with no formal protection (UNEP-WCMC & IUCN, 2019). It is however in one of the most under-collected areas of Sulawesi (Cannon et al., 2007; Kessler et al., 2002) and it is possible that there are more popluations of this species. Following Kartonegoro et al. (2018) it is given a cateogory of Vulnerable under VUD2 to reflect its narrow distribution, occurrence in one of the more threatened forest types in Sulawesi and lack of formal protection (Cannon et al., 2007) and emphasise the need for further collections in this area.

Additional specimens examined. **Central Sulawesi:** Luwuk, Mt Hek, 26 ii 2004*, Hendrian, Newman, Scott, Saleh & Supriadi* 901 (E).

Sulawesi Group: 2 (Atkins et al., Chapter 3).

Notes This species is most similar to the widespread *Cyrtandra polyneura* in its subequal, decurrent leaves, bracteate inflorescence and white flowers with greenish yellow markings in the throat but can be distinguished by its much smaller, narrower leaves; fewer flowers per inflorescence and coarser indumentum on young growth.

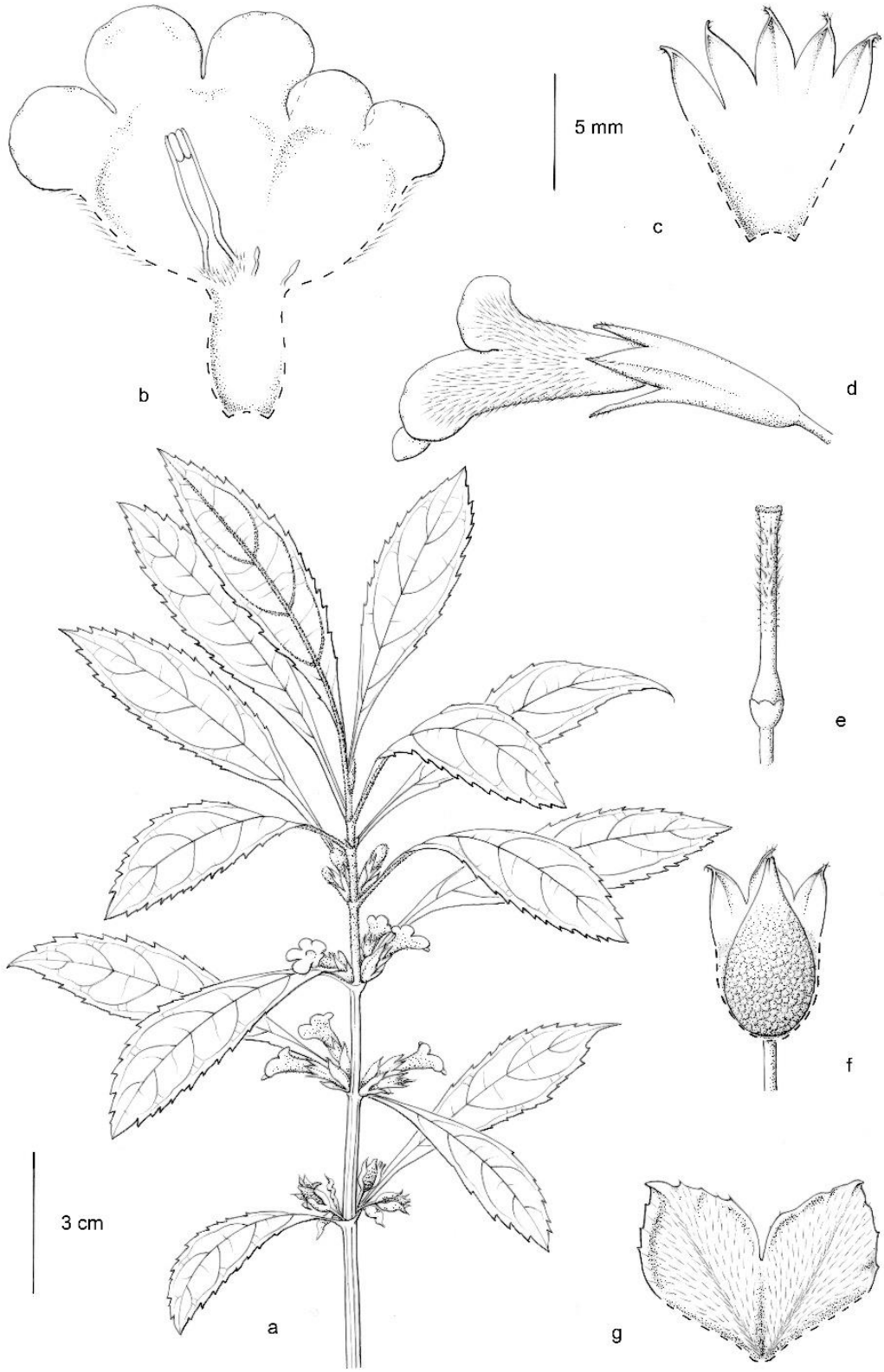


Fig. 2.26 Line illustration of *Cyrtandra hekensis* showing Habit b. Opened corolla showing position of stamens and staminodes c. Opened calyx showing inner surface d. Side view of corolla e. Gynoecium showing disc and top of pedicel f. Fruit with persistent calyx partially removed g. Bracts. Drawn by Claire Banks from *Hendrian* et al. 901. Reproduced from Kartonegoro et al. (2018).

Cyrtandra hendrianii Karton. & H.J.Atkins**,** Edinburgh J. Bot. 75(2): 185 (2018)– Type: Sulawesi, Mt Hek, 660 m, 25 ii 2004, *Hendrian, Newman, Scott, Nazre Saleh & Supriadi 883* (holotype BO; isotype E). **Fig. 2.27**

Shrub to 2 m in height. ***Stems*** striate, reddish, more or less glabrous, slightly hairy in axils. ***Leaves*** opposite, subequal; petioles red, 2–4 cm long, densely hairy when young, becoming more glabrous with age, narrowly winged; blades, 16.4–29.5 x 5.7–9.5 cm, narrow oblong or elliptic to oblanceolate, apex acute to short acuminate, base attenuate, margin serrate; 8–11 pairs of lateral veins and with reticulate tertiary venation; dark green and mostly glabrous above with a few scattered hairs and on the tips of the marginal teeth, paler green below, with red to pink venation, densely fine hairy on midrib and veins with some scattered hairs on the blade. ***Inflorescences*** axillary, subsessile, with c. 8–10 flowers at various stages of development; peduncle 1–2 mm, sparsely hairy; bracts greenish, 25–35 x 5–6 mm, oblong to lanceolate, acuminate, with shallowly serrate margins and a few scattered hairs externally, more densely hairy along the margins and at the apex; bracteoles 15–20 mm long, lanceolate to linear, long acuminate, sparsely hairy, more densely hairy along margins and particularly at the apex; pedicels 5–7 mm long sparsely hairy, extending slightly in fruit. ***Calyx*** tubular, red, 7–8.5 (–10) mm long, appearing 2-lobed, lobes triangular, 3–3.5 (–5) mm long, acuminate, divided very briefly at the apex in to three in the upper lobe and two in the lower, sparsely hairy at the base, more densely so at apex. ***Corolla*** pink, 15–18 mm long, narrow funnelform, lobes rounded, lower lobes slightly more elongate, spreading to somewhat recurved, c. 4 x 3 mm, hairy externally with a dense covering of short glandular hairs internally on the lobes and in the mouth of the corolla. ***Stamens*** with filaments 1.5–2 mm long, attached c. 8 mm from base of corolla, glabrous; anthers c. 1 mm long, glabrous, cohering at apices; staminodes 3, c. 1 mm long. ***Gynoceium*** 10 mm long; disc cupular, 2 mm long, glabrous with undulate margin; ovary glabrous; style with short, glandular hairs particularly towards the apex; stigma bilobed, c. 1 mm across. ***Fruits*** ovoid or rather elongate, glabrous, somewhat verrucose, drying dark brown, 11–15 x 4–7 mm; base of style and calyx persistent.

Distribution. Central Sulawesi (Fig. 2.29).

Habitat and ecology. Hill forest at an altitude of 660–680 m.

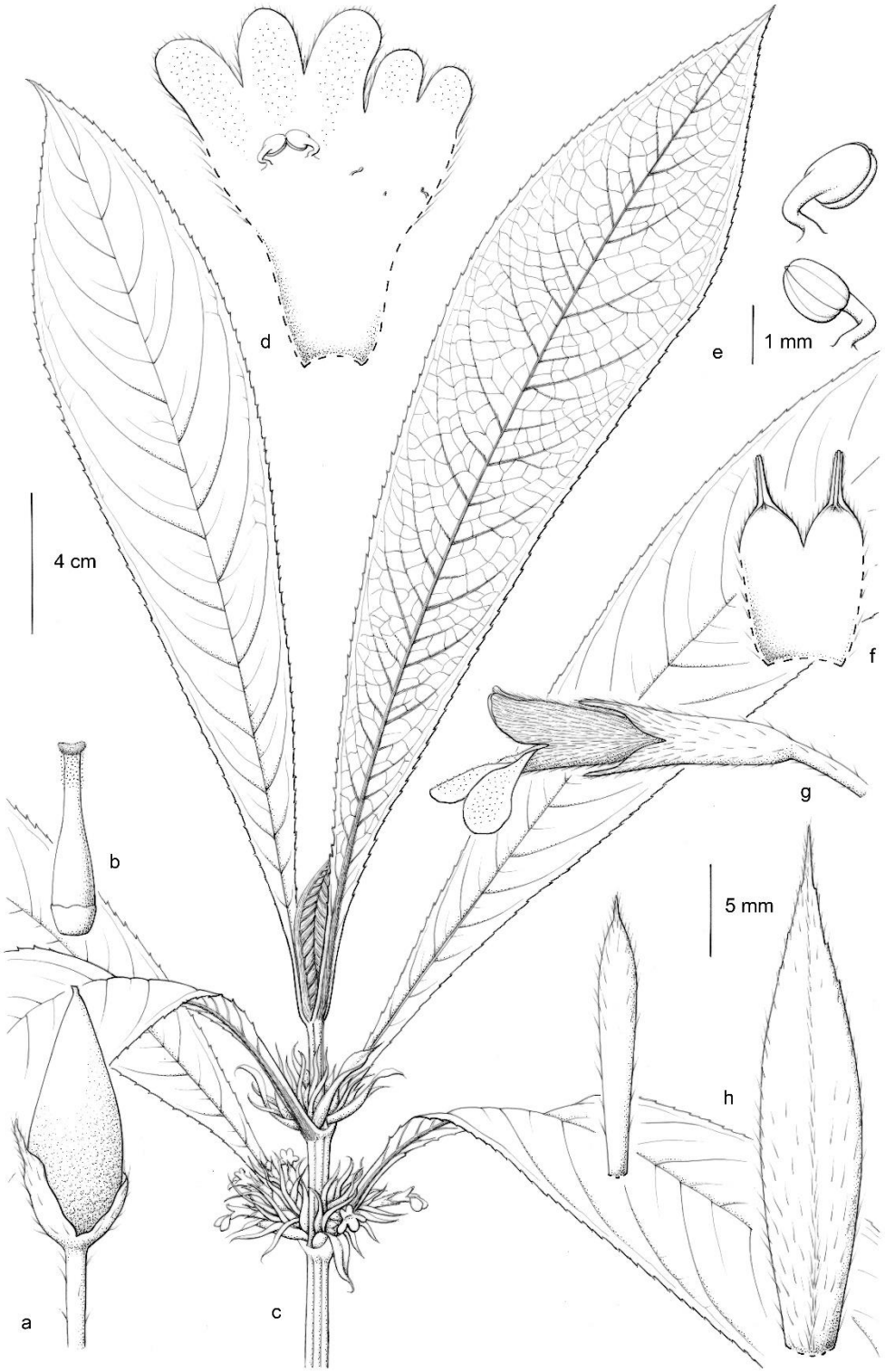


Fig. 2.27 Line illustration of *Cyrtandra hendrianii* showing a. Fruit b. Gynoecium including disc c. Habit d. Opened corolla showing position of stamens and staminodes e. Anthers f. Opened calyx showing inner surface g. Side view of corolla h. Bract and bracteole. Drawn by Claire Banks from *Hendrian* et al. 883. All other parts drawn from Scott 503 (20040646A). Reproduced from Kartonegoro et al. (2018).

Etymology. Named after Hendrian, former Director of Purwodadi Botanic Garden, Java, and also one of the collectors of this new species.

Proposed IUCN conservation category. It has not been possible to calculate an EOO for this species due to the low number of collections but it has an AOO of 8 km^2 a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). This species is known only from Mt Hek, Luwuk Regency where it was collected at relatively low altitude during an expedition in 2004. This forest type is one of the most threatened in Sulawesi (Cannon et al., 2007) and Mt Hek is in an area with no formal protection (UNEP-WCMC & IUCN, 2019). It is however in one of the most under-collected areas of Sulawesi (Cannon et al., 2007; Kessler et al., 2002) and it is possible that there are more popluations of this species. Following Kartonegoro et al. (2018) this species is given a cateogory of Vulnerable under VUD2 to reflect its narrow distribution, occurrence in one of the more threatened forest types in Sulawesi and lack of formal protection (Cannon et al., 2007) and reiterate the need for further collections in this area.

Additional specimens examined. **Central Sulawesi:** Luwuk, Mt Hek, Sungai Spa, 25 ii 2004*, Scott 04-316*, grown at RBGE as accession 20040646A, vouchered as *Scott* 503 (E).

Sulawesi Group: 5 (Atkins et al., Chapter 3).

Notes. This species is most similar to *C. albiflora* collected from the same location. It can be distinguished, however, by its pink corolla and red calyx (vs white corolla and green calyx), more or less glabrous stems (vs densely villous) and oblong-lanceolate bracts, 25-35 mm long (vs linear-lanceolate bracts 10-11 mm long).

Cyrtandra hispidula Karton. & H.J.Atkins, Edinburgh J. Bot. 75(2): 187 (2018) – Type: Sulawesi, Mt Rantemario, 25 iv 2009, *Thomas & Ardi. 09-86* (holotype BO, isotypes E, L). **Fig. 2.28**

Coarse herb to 1.5 m in height. ***Stems*** ridged, striate, green, densely hairy on young growth and around axils, hairs coarse, pale, 1–3.5 mm long. ***Leaves*** opposite, subequal, drying dark brown; petioles green, 2.5–5.5 cm long, densely hairy; blades 14–16 x 9–10 cm, broad elliptic to ovate, apex acuminate, base cuneate, slightly asymmetric, margin serrate; 8–9 pairs of lateral veins and reticulate tertiary venation, dark glossy green, slightly marbled with scattered, long multicellular hairs above, covered with dense, multicellular hairs on midrib and veins below. ***Inflorescences*** axillary, subsessile, 1–2-flowered; peduncle up to 5 mm long, densely hairy; bracts green, 25–40 x 8–20 mm, paired, leaflike, broad elliptic to ovate, with a covering of dense, coarse white hairs, especially on veins, margins serrate, apex acute; pedicels green, 13–15 mm long, hairy, continuing to elongate up to 40 mm with the developing fruit. ***Calyx*** tubular, green, c. 25 mm long, lobes acuminate, lower lobes c. 10 mm long, upper lobes c. 8 mm long, hairy, densely so at the base with a distinctive fringe of hairs. ***Corolla*** white, turning brown with time, tube completely enclosed within calyx, only lobes visible, c. 18 mm long , tube glabrous externally and with a scattering of small glands in the mouth of the corolla, all lobes rounded, lateral lobes with shallowly serrate margins, upper lobes 5–6 x 4 mm, lower and lateral lobes c. 8 x 5 mm. ***Stamens*** with filaments c. 3 mm long, attached c. 8 mm above the base of the corolla, straight, almost glabrous, with a few scattered, glandular hairs; anthers c. 3 mm long, with stalked glandular hairs on the back, not coherent; staminodes 3, c. 2 mm long. ***Gynoecium*** c. 12 mm long; disc cupular with undulate margin, c.2 mm long, glabrous; ovary glabrous; style with some glandular hairs, particularly towards the apex; stigma bilobed, c. 1 mm across. ***Fruits*** oblong, glabrous, smooth, green, drying dark brown, 18–25 x 5–8 mm; calyx and base of style persistent.

Distribution. South Sulawesi: Latimojong Range (Fig. 2.29).

Habitat and ecology. Montane forest at an altitude of c. 2500 m.

Etymology. Named after its distinctive hispid indumentum on most parts of the plant (Kartonegoro et al., 2018).

Proposed IUCN conservation category. It has not been possible to calculate EOO for this species due to the low number of collections but the AOO is 4 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). It is found in montane forest which is not considered to be under threat with a substantial majority of these sites across the island still in good condition (Cannon *et al*., 2007). Following Kartonegoro et al. (2018) a category of Least Concern is proprosed for this species due to the lack of perceived threat.

Additional specimens examined. **South Sulawesi:** Mt Batutoding, 1913*, Rachmat 916* (BO).

Sulawesi Group: 9 (Atkins et al., Chapter 3).

Notes. The combination of coarse, hispid, white indumentum, broad leaves and large, leaf-like inflorescence bracts distinguishes this species from any other *Cyrtandra* species on the island.

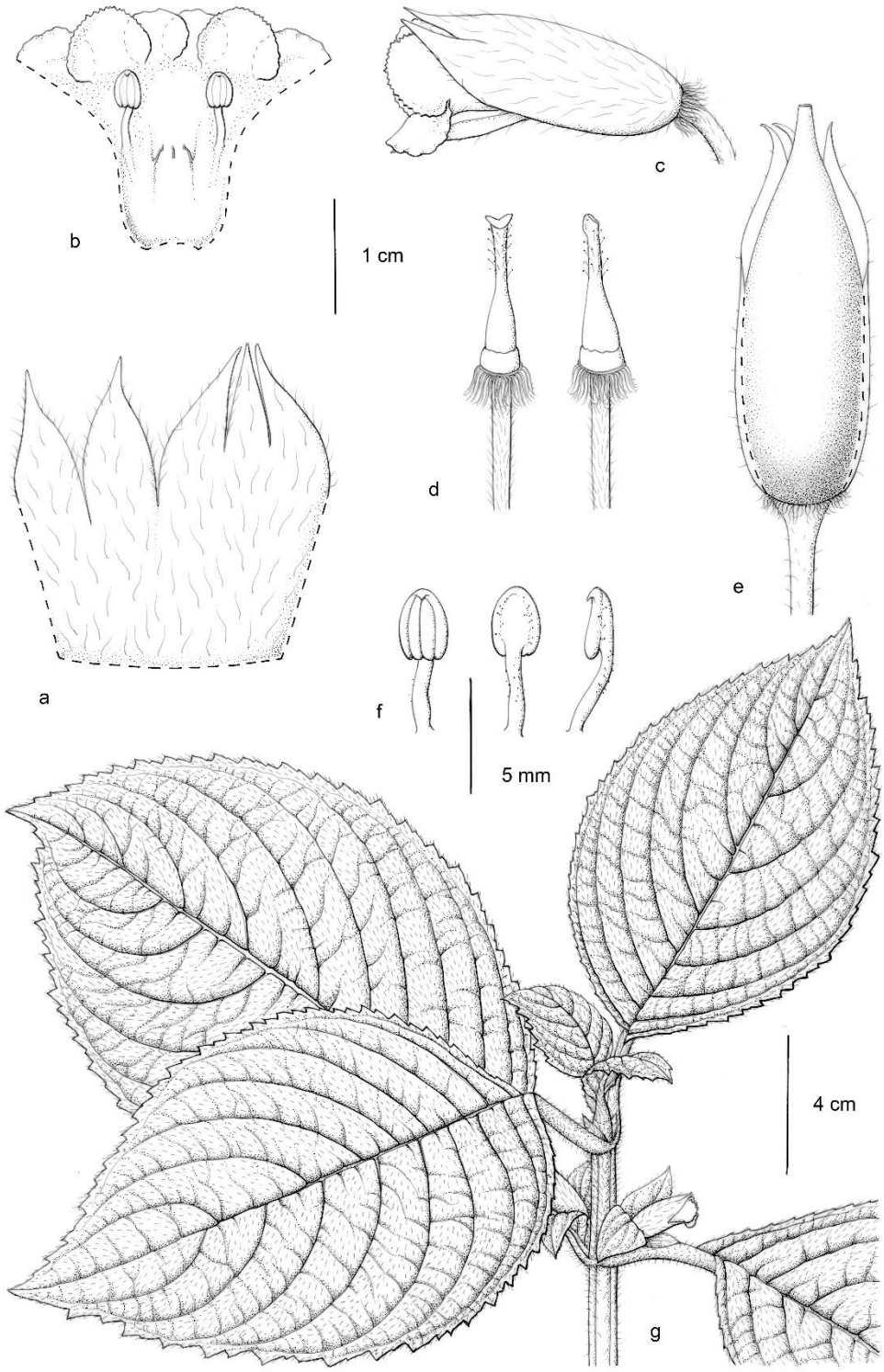


Fig. 2.28 Line illustration of *Cyrtandra hispidula* showing a. Opened calyx showing outer surface b. Opened corolla showing position of stamens and staminodes c. Side view of corolla d. Gynoecium including disc and top of pedicel e. Fruit with persistent calyx partially removed f. Anthers g. Habit. Drawn by Claire Banks from Thomas & Ardi 09-86. Reproduced from Kartonegoro et al. (2018).

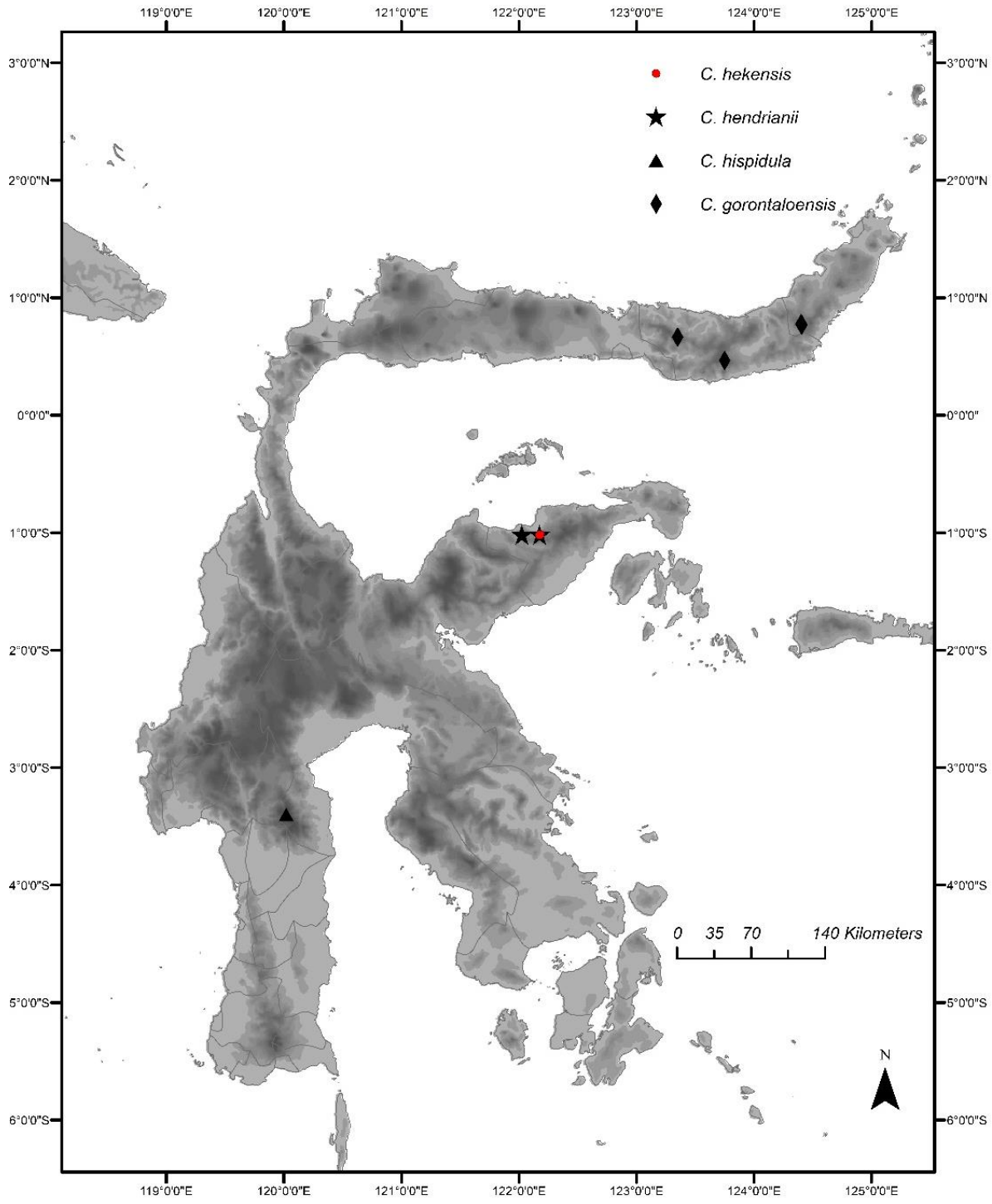


Fig. 2.29 Distribution of *Cyrtandra gorontaloensis* (black diamonds), *C. hekensis* (red circles), *C. hendrianii* (black stars) and *C. hispidula* (black triangles).

Cyrtandra hypogaea Koord., Meded's. Land. Plantent. 19: 628 (1898) Type: Celebes [Sulawesi], Mt. Lolomboelan, 9 iv 1897, *Koorders* 17190B (lectotype BO hic desig.; isolectotype L). **Fig. 2.30**.

Branching herb or ***shrub*** to 2 m in height, rarely epiphytic (*de Vogel* 2649). ***Stems*** striate, subglabrous, hairy on young growth, woody at base. ***Leaves*** opposite; both members of a pair well developed but somewhat unequal in size; petiole 10–35 mm, hairy to densely hairy; blades (5–)10–25 cm × (1.5–)3.5–6 cm, usually narrow obovate, sometimes narrow oblong or narrow oblanceolate, apex acuminate, base acute, asymmetrical, briefly decurrent, margin serrulate to serrate; 5–7(–8) pairs of lateral veins, curving upwards and running out to margin, sometimes with short lateral veins running out to adjacent teeth, sparsely hairy above, hairy below, more densely so on midrib, veins and margins. ***Inflorescences*** on trailing stems from base of main plant; trailing inflorescence stem 2–3 mm in diameter, up to 2 m long, glabrous, usually appearing 'notched' from the remnants of old bracts; bracts 3–5 mm × 1–2 mm, ovate, acuminate at apex, hairy, not connate, caducous. ***Calyx*** purple or reddish, 6–10 mm long, evenly five-lobed or bilabiate with three lobes joined to half way, lobes linear, 6–8 mm or divided briefly at apex,hairy externally. ***Corolla*** white flushed pink with deep red guidelines and light yellow or orange in the throat or, rarely, bright red with (or without) yellow in the throat, 8–15 mm long, more or less parallel-sided, widening at mouth, lobes not recurved, lobes 3–4 mm × 2–3 mm, hairy externally. ***Stamens*** with filaments 1–2 mm long, attached 4–7 mm from base of corolla; anthers 1 mm long, connected at apices before dehiscence, staminodes 3, laterals c. 1 mm long, central 0.5 mm long. ***Gynoecium*** 4–7(–10) mm long; disc unilateral with undulate to lobed margin, 1–2 mm long, glabrous; ovary subglabrous to sparsely hairy; style eglandular hairy for whole length; stigma bilobed, lobes vertical, 1–2 mm long, densely glandular on inner surface of lobes. ***Fruits*** ovoid to narrow ovoid, green when unripe, sometimes recorded as turning reddish, glabrous, distinctively tesselate when dried, 9–12(–15) mm × 2–5 mm, calyx and base of style usually persistent.

Distribution. North Sulawesi, Gorontalo, Central Sulawesi, South Sulawesi, South East Sulawesi, West Sulawesi. (Fig. 2.31).

Habitat and ecology. Lowland, Hill and Upland Forest at an altitude of 50-1290 m.

Etymology. The epithet of this species refers to the position of the flowers near the ground (Koorders, 1898).

Proposed IUCN conservation category. The EOO of this species is 173,191 km^2 and the AOO is 112 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). This is one of the most common and widespread species on the island, collected in all of the six provinces and over a wide altitudinal range and for this reason is considered to be of Least Concern.

Additional specimens examined: **North Sulawesi**. Bolaang Mongondow, Kasingolan River, 30 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK17 (BO, E); Mt London, 31 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK30 (BO, E); Minahassa, Wagio crater, Mount Mahawae, Tomohon, 4 vii 1956, *Forman* 393 (BO, L); Gunung Mahawu, 15 ii 2009, *Girmansyah* 1257 (BO); South part of Wiau forest reserve, base of Gunung Klabat, 1 xi 1973, *de Vogel* 2649 (BO, CANB); Bolaang Mongondow, Dumoga Bone National Park, 28 iii 1985, *de Vogel & Vermeulen* 6786 (E, L);

Gorontalo. Route along the Olama River to Gunung Gambuta, 9 iv 2002, *Scott* 02-42, grown at RBGE as accession 20021875A, vouchered as *Atkins* 46 (E);

Central Sulawesi. Pangi Binangga, Uwe Lutu, CA, 20 vii 2018, *Ardi* WI209 (KRB); Gunung Nokilalaki, track to shelter 2, 24 vii 2018, *Ardi* WI222 (KRB); Danau Poso, Tentena-bancea road divide, 2 viii 2018, *Ardi* WI277 (KRB); Upper Sopu River, E. end of Sopu Valley, 5 v 1979, *van Balgooy* 3501 (L); Lore Lindu National Park, Ponoh, 3 km NE of Toro Village, 17 xii 2007, *Cicuzza* 620 (E); Lore Lindu, Mt Nokilalaki, 6 iii 2008, *Cicuzza* 793 (E); Lore Lindu National Park, Ponoh, 3 km NE of Toro Village, 10 iv 2008, *Cicuzza* 1016 (E); Luwuk area, inland from Batui, 17 x 1989, *Coode* 5983 (A, BO, K, L, SING); Luwuk District, Bunta Subdistrict, Sumber Agung, Gunung Hek, 26 ii 2004, *Hendrian, Newman, Scott, Saleh & Supriadi* 900 (E); Sopu Valley, c.80 km s. of Palu, 6 v 1979, *Hennipman* 5621 (BO, E); W of Tongoa, 6 iii 1981, *Johansson*, *Nybom & Riebe* 195 (L); Pass between Lake Poso and Wotu, 2 iii 2000, *Mendum, Argent & Hendrian* 00220 (BO, E); Between Palu and Parigi, 35 km from Palu, 7 iv 1975, *Meijer* 9342 (BO, L); G. Dako, Teluk Bone, Lakatan, 24 iii 1985, *Ramlanto & Zainal Fanani* 513 (BO); Luwuk District, Bunta Subdistrict, Sumber Agung, Gunung Hek, 26 ii 2004, *Scott* 04-329, grown at RBGE as accession 20040647A, vouchered as Scott 449 (E); Mt Roroka Timbu, 11 v 1979, *de Vogel* 5296 (L); Sopu valley c. 80 km SSE of Palu, 26 v 1979, *de Vogel* 5578 (BO, L);

West Sulawesi. Gunung Gandan Dewata, 20 iv 2016, *Kartonegoro, Ardiyani, Santoso Wardani* ARK904 (BO, E);

South Sulawesi. Wawmseru Mt., SW of Soroako, 3 vi 1979, *Hennipman* 5994 (BO, E); Kawata, 18 ix 1929, *Kjellberg* 2334 (BO, S); Rante Angin subdistrict, Tinukari village, 30 vi

2011, *Widjaja, Sujadi, Santoso & Hapid* EAW9713 (BO); Tinukari village, 30 vi 2011, *Widjaja, Sujadi, Santoso & Hapid* EAW9717 (BO);

South East Sulawesi. Selewar, Preko, 5 x 1929, *Kjellberg* 2498 (BO, S); Bulu Porema, 27 x 1929, *Kjellberg* 2664 (BO, S).

Sulawesi Group: 4 (Atkins et al., Chapter 3).

Notes: Cyrtandra hypogaea can be easily distinguished from other species on Sulawesi with trailing inflorescences, by a thicker, and usually more notched, inflorescence stem 2–3 mm in diameter, smaller flowers, and a unilateral disc. The fruits also have a distinct, tesselate appearance when they are dried.

Koorders did not specify a type when he described this species so the most complete of Koorders own collections, *Koorders* 17190B in the herbarium in Bogor (BO), annotated by him with the name *Cyrtandra hypogaea* and with an illustration attached, has been selected as the lectotype.

Fig. 2.30 Plate of *Cyrtandra hypogaea* showing a. fruit b. trailing inflorescence stems with immature fruits c. habit d. side view of flowers e. front view of flowers. Photos: a Hannah Atkins (RBGE living accession 20040647), b-e Sadie Barber (*Barber* et al. BAKK 30).

Cyrtandra jellesmani Koord., Meded.'s Land. Plantent. 19: 628 (1898). – Type: Celebes [Sulawesi], Minahassa, Pinamorongan camp, 26 i 1895, *Koorders* 17193 (lectotype BO hic desig.).

Herb to 30 cm in height. ***Stems*** striate, sparsely hairy, more densely so on young growth. ***Leaves*** opposite; both members of a pair well developed but unequal in size, blades 4–14 cm × 1.5–3.5 cm, oblanceolate to narrow oblanceolate, apex shortly acuminate, base decurrent, plicate, margin crenate-serrulate; 3–5 pairs of lateral veins, curving upwards and running out to margin, glabrous above, sparsely hairy below, more densely so on midrib and veins. ***Inflorescences*** axillary**,** subsessile, 1-flowered; bracts 8–10 mm × 1mm, linear, hairy, not connate, pedicels 1 mm, hairy. ***Calyx*** 12–15 mm long, 2-lobed, lobes triangular, acuminate at apex, 7–8 mm long, hairy externally. ***Corolla*** white, 45 mm long, funnel-shaped, lobes not strongly recurved, lower lobes up to 11 mm × 10 mm, upper lobes 10 mm × 9 mm, hairy externally. ***Stamens*** with filaments 11 mm long, attached 25 mm above base of corolla, glabrous; anthers 1.5–2 mm long, connected at apices and face to face before dehiscence; staminodes not seen. ***Gynoecium*** 25 mm long; disc 1 mm long, cupular with lobed margin, glabrous; ovary eglandular hairy, glabrous towards base; style densely eglandular hairy for whole length; stigma peltate, 2 mm across. ***Fruit****s* not seen.

Distribution. North Sulawesi (Fig. 2.35).

Habitat and ecology. Lowland and hill forest at an altitude of 500-600 m.

Etymology. This species was named after Mr Jellesman, a resident of Manado whom Koorders visited in 1895 (Koorders, 1898).

Proposed IUCN conservation category. The low number of collections means that an EOO for this species could not be calculated but the AOO is 8 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). This species is only known from two collections from North Sulawesi, collected in 1895 and 1917. We returned to these localities in 2016 and were unable to find any populations. Lowland and hill forest are the most threatened forest

types on the island (Cannon et al., 2007), and much of the forest surrounding the type locality is now gone. For these reasons, this species is considered to be Critically Endangered.

Additional specimens examined: **North Sulawesi**. Minahassa, Goeroepahi, 15 iv 1917, *Kaudern* 46 (S, L).

Sulawesi Group: 3 (Atkins et al., Chapter 3).

Notes: This is a distinctive species with its oblanceolate leaves and large, funnel shaped flowers. Koorders' only collection, *Koorders* 17193, is designated here as the lectotype.

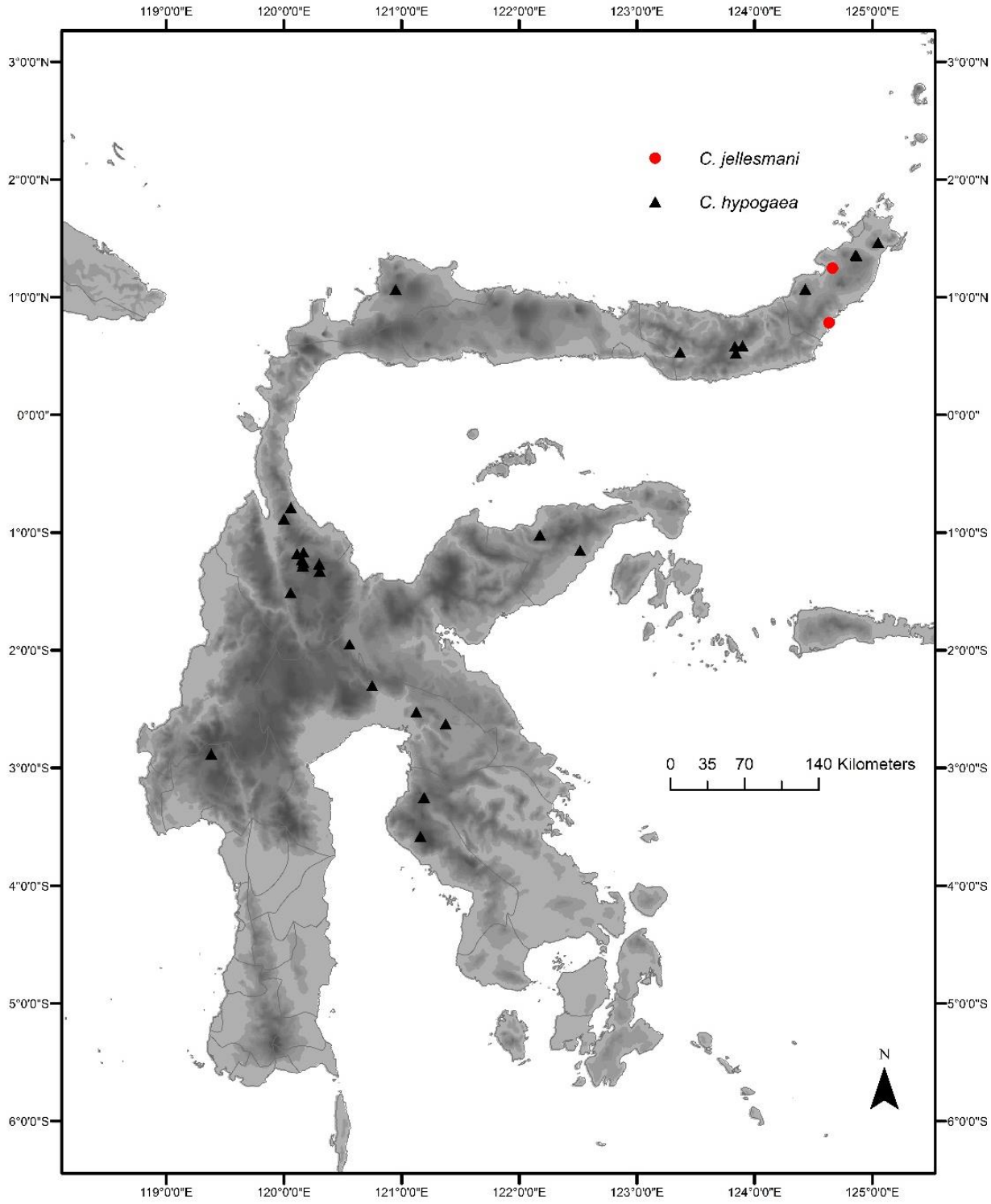


Fig. 2.31 Distribution of *Cyrtandra hypogaea* (black triangles) and *C. jellesmani* (red circles).

Cyrtandra kinhoii Karton. & H.J.Atkins, Edinburgh J. Bot. 75(2): 190 (2018) – Type:Sulawesi, Mt Ambang Nature Reserve, Paya Paya, near Sinsingon village, 2 xi 2016, *Barber, Atkins, Kartonegoro & Kinho.* BAKK 36 (holotype BO , isotype E, L.) **Fig. 2.32**

Shrub 1–3 m or ***small tree*** 6–7 m in height. ***Stems*** tesselate, glabrous, sparsely hairy on younger growth, woody. ***Leaves*** opposite; subequal to somewhat unequal; petioles 1.5–2 cm long, winged; blades 30–60 × 10–15 cm, elliptic to obovate to oblanceolate, usually crowded at the ends of branches, apex short-acuminate, rarely obtuse, base attenuate, margin serrate; 10–20 pairs of lateral veins and reticulate tertiary venation, curving upwards and running out to the margin, occasionally branching near the margin, glabrous, midgreen above, sparsely hairy and paler green below, more densely hairy on midrib and veins and occasionally flushed red at base of leaf. ***Inflorescences*** axillary, subsessile, congested, with up to c. 15 flowers at various stages of development; bracts oblong-lanceolate, light green, flushed slightly reddish, leathery, 3–4.5 x 2–2.5 cm, subglabrous to sparsely hairy, slightly warty, apex acute or short-acuminate, caducous; bracteoles lanceolate, light green, subglabrous c. 3 x 1 cm, leathery, apex acuminate; pedicels 4–7 mm long, light green, glabrous to sparsely hairy. ***Calyx*** tubular, 21–25 mm long, light green to dark reddish-brown, sparsely hairy, warty at base, lobes acuminate, lower lobes divided c. 12 mm from apex, upper lobes less deeply divided, 8–10 mm from apex, densely hairy. ***Corolla*** white or flushed slightly pink, 30-35 mm long, narrow in basal third to half, gradually widening to mouth, glandular hairy on outer surface, densely so on inner surface, lobes strongly recurved, upper lobes rounded, 6 x 5 mm, lower and lateral lobes rounded to slightly oblong, 5–10 × 5–7 mm, lobes with dense covering of glandular hairs. ***Stamens*** with filaments 2–8 mm long, attached 12–20 mm above the base of corolla, glabrous, light green; anthers 2–3 mm, coherent at apices, cream; staminodes 3, laterals c. 1.5 mm long, central c. 0.5 mm long. ***Gynoecium*** 25–30 mm long; disc cupular with undulate margin, lower on one side, glabrous, 2–3 mm; ovary glabrous; style white, glabrous, becoming slightly hairy towards apex on some collections; stigma light green, bilobed, lobes 3–4 x 2–3 mm across, vertical or spreading, densely glandular hairy on inner surface of lobes. ***Fruits*** ovoid, glabrous, 10–15 × 5–8 mm, green when unripe; bracts and calyx not persistent, base of style occasionally persistent.

Distribution. North Sulawesi and Gorontalo (Fig. 2.35).

Habitat and ecology. Hill and upland forest at an altitude of 700–1300 m.

Etymology. Named after Julianus Kinho, researcher at the Forestry Research Institute of Manado, North Sulawesi and one of the collectors of the type specimen.

Proposed IUCN conservation category. Based on this species current distribution, now confined to the northern arm, the EOO of this species is 4,053 km^2 and the AOO is 32 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011). Some of the collections fall within the Bogani Nani Wartabone National Park and the Gunung Ambang Nature Reserve (UNEP-WCMC & IUCN, 2019) and will receive some protection but the remaining populations are from the more densely populated areas around Manado and Tomohon. Given the restricted distribution of this species and its proximity to some of the more heavily populated areas of Sulawesi, this species is considered Vulnerable under the VUD2 category.

Additional specimens examined. **North Sulawesi.** G. Manimporok, Soputan Mts, 18 vi 1954, *Alston* 15926 (BM, BO); East Bolaang Mongondow, Mt Ambang, 3 xi 2016, *Barber* et al. BAKK 65 (BO, E); Tomohon, Mt Mahawu, 23 vi 1956, *Forman* 223 (BO, K, L); Minahasa Regency, Mt Masarang, 10 i 1895, *Koorders* 17187B (BO, L); Lolombulan, 6 iv 1895, *Koorders* 17191 (BO, L);

Gorontalo. Mt Gambuta, 10 iv 2002, *Atkins* et al. 56 (BO, E).

Sulawesi Group: 10 (Atkins et al., Chapter 3).

Notes. This species is similar vegetatively to *C. fasciata, C. flavomaculata* and *C. longistamina* in having decurrent leaves and tesselate stems. It can be distinguished most easily from *C. fasciata* by its larger inflorescence bracts (25 mm wide as opposed to 2 mm wide) and from *C. longistamina* by its ovoid fruits on short pedicels up to 7 mm long as opposed to sub-globose fruits on pedicels up to 30 mm long.

When this species was first described (Kartonegoro et al., 2018), three outlier collections from Lore Lindu in Central Sulawesi were highlighted as having a different style indumentum. Recent collections with photographs from Lore Lindu have provided further information and it is now clear that these collections represent a different species, *Cyrtandra flavomaculata*. The new species can be distinguished from *C. kinhoii* by its corolla which is funnel shaped as opposed to tubular, white with large yellow markings on its upper and lower lobes as opposed to white or flushed pink without markings and with a densely hairy, not glabrous, style.

The young leaves of *C. kinhoii* are reported to be collected and used as a vegetable (Atkins, pers. comm.).

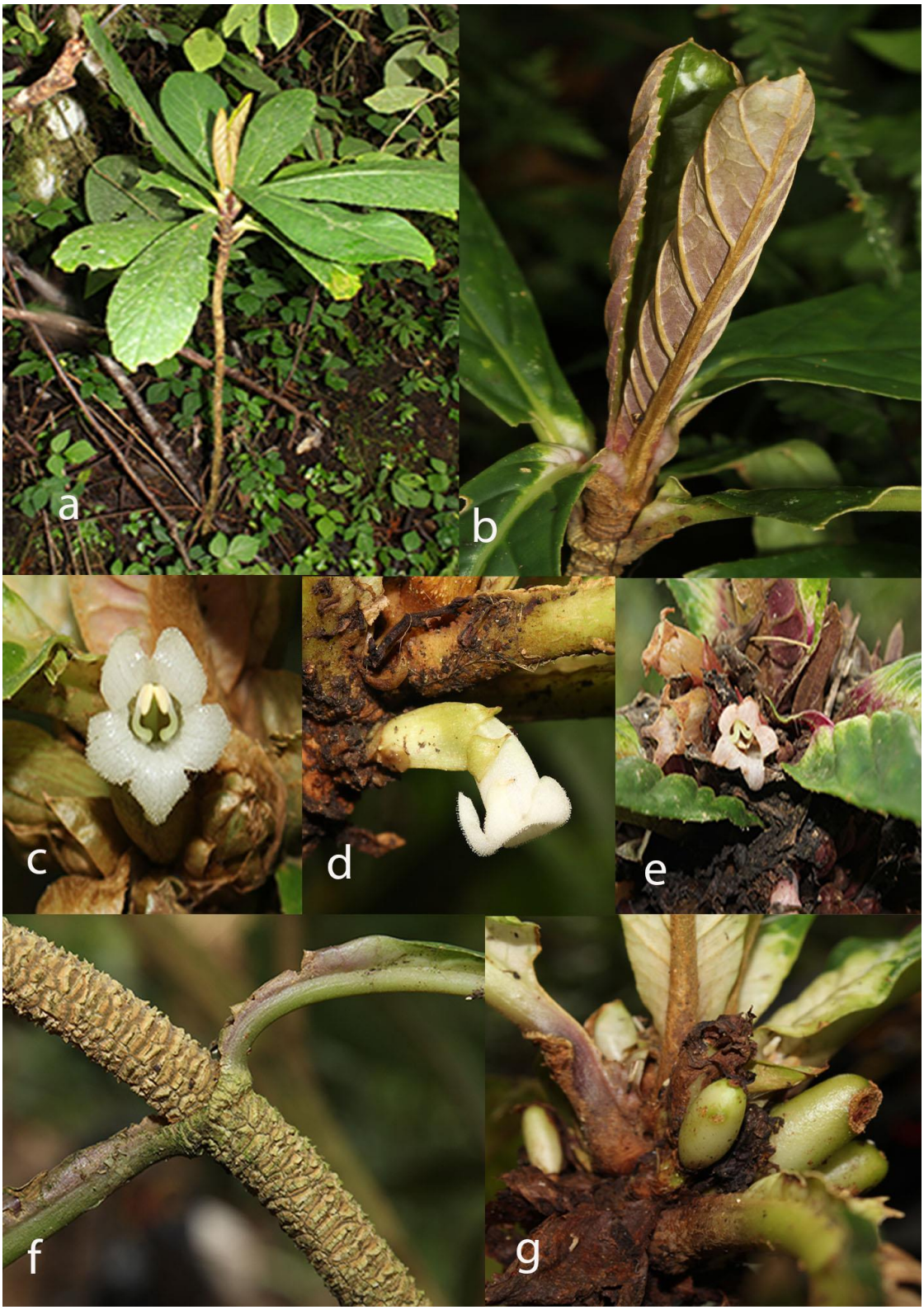


Fig. 2.32 Plate of *Cyrtandra kinhoii* a. habit b. young leaves c. front view of young flower d. side view of young flower e. view of older flower in inflorescence f. tesselate stem g. young fruits. Photos: Sadie Barber. Reproduced from Kartonegoro et al. (2018).

Cyrtandra kjellbergii R.Bone & H.J.Atkins, Edinburgh J. Bot. 70(3): 460 (2013) − Type: Sulawesi, B. Poka Pindjang, 27 v 1929, *Kjellberg* 1459 (holotype BO; isotype S). **Fig. 2.33**

Shrub (height not recorded). ***Stems*** glabrescent, densely hairy when young. ***Leaves*** sub-equal to markedly anisophyllous; petiole 4–6 mm long, sparsely hairy; blades of larger leaf, 4–6 × 1.9–3 cm, elliptic to obovate, apex acuminate, base cuneate, margin deeply lobed with c. 3–7 lobes along each side, lobes acute, sparsely ciliate; 4–5 pairs of lateral veins, upper surface very sparsely pilose, lower surface sparsely hairy on primary and secondary veins, glabrescent between veins. ***Inflorescences*** sessile in leaf axils or at the base of plant, 1–2-flowered; bracts c. 2 mm, often caducous, elliptic to ligulate, hairy; peduncle absent; pedicels 5–10 mm, sparsely hairy. ***Calyx*** c. 6–11 mm long; lobes caudate,c. 2–5 mm long, hairy externally. ***Corolla*** yellow, 28 mm long, tube narrow, more or less parallel-sided, widening slightly towards mouth, lobes oblong, 5mm x 3-4.5 mm, hairy on outer surface, glabrous on inner surface with some glandular hairs at base of lobes. ***Stamens*** with filaments 9–10 mm long, attached c. 17 mm from base of corolla, glabrous; anthers 1–1.5 mm long; staminodes 3 mm long, one highly reduced, glabrous. ***Gynoecium*** 16–20 mm long; disc cupular, undulate, c. 1 mm long, glabrous externally; ovary densely hairy; style glabrescent to sparsely glandular-hairy; stigma capitate, 1 mm across, papillose. ***Fruits*** ovoid, 12–13 mm × 4–5 mm, sparsely hairy, calyx and base of style persistent.

Distribution. South Sulawesi (Fig. 2.35).

Habitat and ecology. Montane forest at an altitude of 2300 m.

Etymology. This species is named after Gunnar Konstantin Kjellberg (1885-1943) who made an important botanical investigation of Sulawesi in 1929 (Bone & Atkins, 2013).

Proposed IUCN conservation category. This species is only known from one location so it has not been possible to calculate EOO but it has an AOO of 4 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011). The species is only known from the type location, collected in 1929 at 2300 m asl. The collection locality is not in a protected area or National Park (UNEP-WCMC & IUCN, 2019) but was collected in montane forest which is one of the least threatened forest types on the island (Cannon et al., 2007). A category of Least Concern is assigned for for this species as there is no evidence of threat but the importance of further collecting in this area is emphasised.

Additional specimens examined. This species is known only from the type collection.

Sulawesi Group: 14 (Atkins et al., Chapter 3).

Notes. This species is similar in overall appearance to *C. balgooyi* from Central Sulawesi. It can be distinguished by leaf margin (deeply lobed vs serrate), corolla size (28 mm vs 20 mm long) and style indumentum (glabrescent to sparsely glandular-hairy vs densely eglandular hairy). It is also currently only known from the Latimojong Mountains while *C. balgooyi* is restricted to the environs of the Lore Lindu National Park in Central Sulawesi.

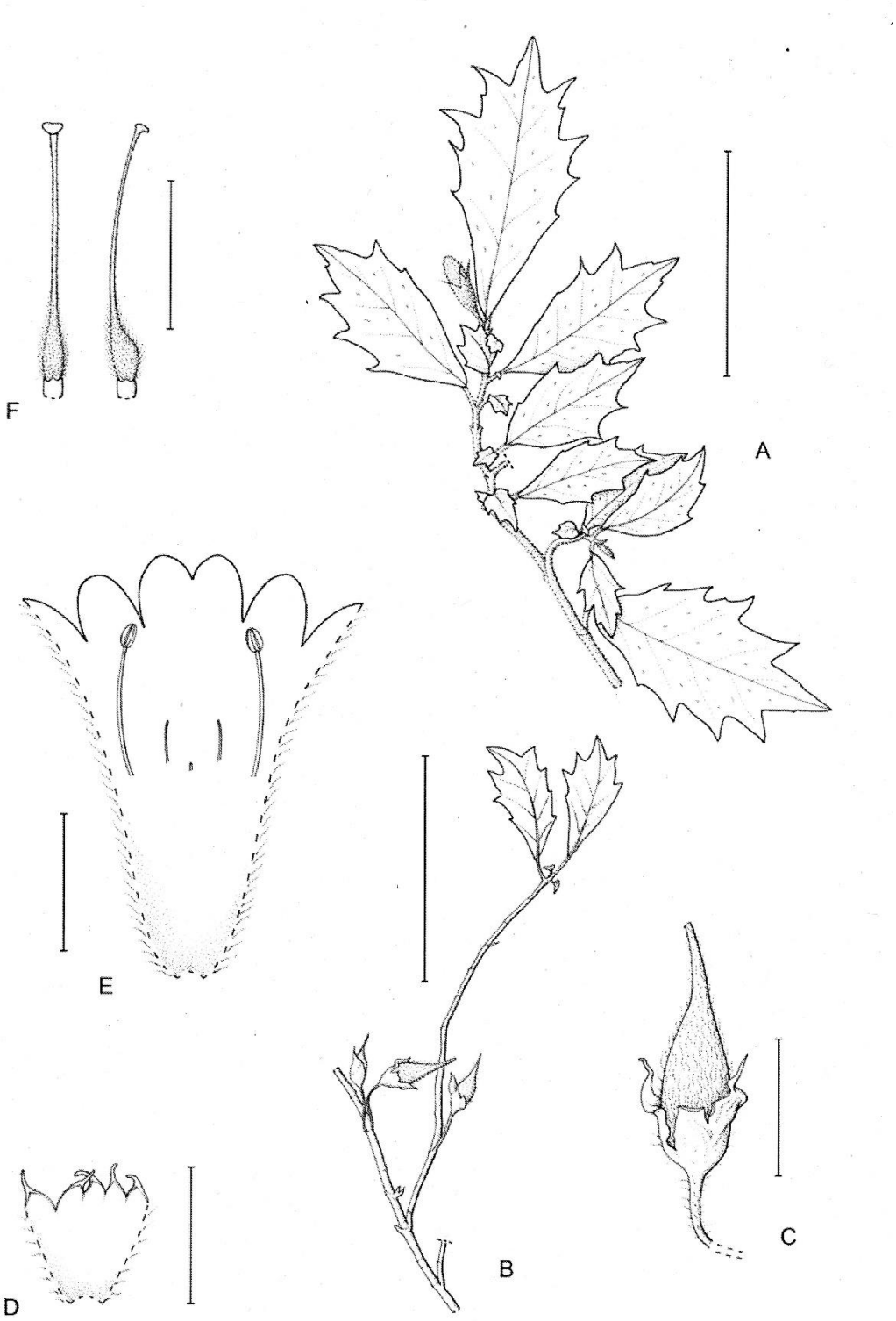


Fig. 2.33 Line illustration of *Cyrtandra kjellbergii* showing a. Habit b. Fruits on stem c. Fruit and calyx d. Opened calyx showing inner surface e. Opened corolla showing position of stamens and staminodes f. Gynoecium and disc. Drawn by Claire Banks from *Kjellberg* 1459. Reproduced from Bone & Atkins (2013).

Cyrtandra longirostris de Vriese, Pl. Ind. Bat. Orient.: 12 (1856). – *Rhynchocarpus longirostris* Reinwardt ex de Vriese in Pl. Ind. Bat. Orient. 12 (1856). nom. inval. - Type: Celebes [Sulawesi], in monte Lujong insulae, *Reinwardt* 1535 (lectotype L hic. desig.; isolectotype S).

Shrub to 2m in height. ***Stems*** striate, hairy, more densely so on young growth, woody at base. ***Leaves*** opposite, both members of a pair well developed but somewhat unequal in size; petiole 5–15 mm, hairy; blades 7–19 cm × 2.5–7 cm, elliptic to narrow elliptic, sometimes obovate, apex acuminate, base acute, briefly decurrent, slightly asymmetrical, margin subentire to serrulate; 6–8 pairs of lateral veins curving upwards and running out to margin, sparsely hairy above and below, more densely so on midrib and veins below. ***Inflorescences*** axillary, pedunculate, 2–3-flowered; bracts 2–3 mm × 1–2 mm, lanceolate, hairy, not connate. peduncles 15–40 mm, sparsely hairy to hairy; pedicels 8–12 mm, sparsely hairy. ***Calyx*** 7–9 mm, evenly 5-lobed, rarely 4-lobed, lobes triangular, acuminate at apex, 4–6 mm, hairy externally. ***Corolla*** white or light yellow, 11–17 mm long, tube narrow in basal half, widening abruptly to mouth in apical half, lobes not recurved, upper lobes 4 mm × 3–5 mm, lower lobes 6 mm × 3 mm, hairy externally. ***Stamens*** with filaments 2–3 mm long, attached 5–8 mm from base of corolla, glabrous; anthers 1 mm long, connected at apices before dehiscence.; staminodes 1–2 mm long. ***Gynoecium*** 8–10 mm long; disc cupular, margin undulate, 1 mm long, glabrous externally; ovary glabrous; style glabrous towards the base, becoming glandular hairy at the top of the style near the stigma; stigma slightly bilobed, lobes almost triangular, 1 mm across. ***Fruits*** ovoid, 5 mm × 3 mm, glabrous, bracts, calyx, style and stigma persistent.

Distribution. North Sulawesi (Fig. 2.35).

Habitat and ecology. Hill and upland forest at an altitude of 700-1100 m

Etymology. This species is named for the 'beaked' appearance of the fruits where they are tipped by the persistent style.

Proposed IUCN conservation category. This species has an EOO of 931 km^2 and an AOO of 16 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011). It grows at relatively low altitudes in one of the most threatened forest types (Cannon et al., 2007), in one of the most densely populated areas of Sulawesi where there is no formal protection (UNEP-WCMC & IUCN,

2019). Despite it being one of the best collected areas on the island, this species has only been collected six times, the last time being in 1954. Due to the restricted distribution, threat from intensive agriculture and urban expansion (Cannon et al., 2007) and the lack of any formal protection, this species is considered to be Endangered under the B2a criteria.

Additional specimens examined: **North Sulawesi**. Summit of G. Empong, 7 vii 1954 *Alston* 16280 (A, BM, BO); Tondano, 1840--1842, *Forsten* 157 (K, L); Minahassa, Ratahan, 13 iii 1895, *Koorders* 17182 (BO, L); Lolomboelan, 6 iv 1895, *Koorders* 17186 (BO, L); Ratahan, 13 iii 1895, *Koorders* 17196 (BO, L).

Sulawesi Group: 5 (Atkins et al., Chapter 3).

Notes: This species can be distinguished in Sulawesi by its combination of subequal leaves, long pedunculate inflorescences and ovoid fruits with persistent styles. It is morphologically similar to *C. cuneata* Blume from Ternate and *C. calyptribracteata* Bakh.f. from Java and is often misidentified as these. As some of these names have been linked with collections from Sulawesi we clarify their differences and nomenclatural history here.

The Sulawesi species, *C. longirostris,* has small inflorescence bracts (3 mm long), glabrous fruits and white flowers; *C. cuneata* from the Moluccas has large inflorescence bracts (10-15 mm long) that are not connate, hairy fruits and purplish flowers and *C. calyptribracteata* has ovate, connate bracts (10-15 mm long) that completely enclose the young inflorescence, glabrous fruits and reddish or pink flowers.

The first of these names to be published was *C. cuneata* by Blume in 1826. He did not cite any specimens but gave the distribution of the species as the Moluccas. The only specimen that was collected early enough to have been seen by Blume from the Moluccas is *Reinwardt* 1101 at Leiden (L2818385).

In 1856, De Vriese published the names *C. longirostris* and *C. umbellata* with no reference to *C. cuneata. Cyrtandra longirostris* was described from Sulawesi and a specimen with the details ‘In monte Lujong insulae Celebes’ was cited below the description. This matches a *Reinwardt* collection at Leiden (L0277503) which also has the manuscript name *Rhynchocarpus longirostris* written on it and this is selected here as the Lectotype of *C. longirostris.*

Under *C. umbellata,* de Vriese listed specimens from both Sulawesi and Ternate (de Vriese, 1856). The specimen from Sulawesi was a *Reinwardt* collection with the locality details 'Inter Lotam et Kaskassan'. This matches a sheet in the herbarium in Leiden (L0003287) and is, in fact, *C. longirostris* having small inflorescence bracts and glabrous fruits and is listed under *C. longirostris* here. The specimen from Ternate is described as 'In sylvis montis Idjeng' which matches *Reinwardt* 1101 (L2818385), the type of *C. cuneata*.

Clarke (1883) recognised that *C. umbellata* was a synonym of *C. cuneata.* However he incorrectly listed specimens from Sulawesi and Java under *C. cuneata*. The Javanese material was later separated and described as *C. calyptribracteata* (Bakhuizen van den Brink, 1950) and the Sulawesi specimen that Clarke cited under *C. cuneata* is moved here to *C. longirostris.*

The name *C. umbellata* is also later used illegetimately by Kraenzlin for a completely unrelated Philippine species (Kraenzlin, 1913) and is subsequently re-named *C. bacanii* Olivar & Muellner-Riehl (Olivar & Muellner-Riehl, 2019).

Cyrtandra longistamina H.J.Atkins & Karton. **sp. nov.** ined.

Similar to *Cyrtandra fasciata* H.J.Atkins in its tesselate, scaly stem and decurrent leaves but distinguished by corolla colour (corolla creamy white or yellow with no stripes in *C. longistamina* vs corolla yellow with red stripes in *C. fasciata*), pedicel length (pedicel 15–30 mm long in *C. longistamina* vs pedicel 4–5 mm long in *C. fasciata*), calyx length (calyx 15 mm long in *C. longistamina* vs calyx 28 mm long in *C. fasciata*) and calyx texture (calyx membranaceous and not ridged in *C. longistamina* vs calyx leathery and strongly ridged in *C. fasciata*) – Type: Sulawesi, Gunung Sojol, 27 ii 2000, *Mendum* et al. 00197 (holotype E; isotype BO). **Fig. 2.34**

Woody herb, shrub or small tree 3-6 m in height. ***Stems*** tesselate, scaley, glabrous. ***Leaves*** opposite; those of a pair subequal; petioles 3–9 cm long, hairy towards base, particularly on young growth; blades 10–35 cm × 5–11 cm, narrow oblong, apex short acuminate, base attenuate, narrowly winged, more or less symmetrical, margins serrulate to serrate; 10–15 pairs of lateral veins and reticulate tertiary venation; subglabrous above, hairy towards base of petiole, sparsely hairy below, more densely so on midrib and veins and base of petiole. ***Inflorescences*** axillary, sessile, 2-6-flowered; bracts light green, 20 mm × 10 mm, ovate with slightly serrate margins, acuminate at apex, overlapping but not connate, glabrous; bracteoles similar to bracts but smaller and narrower;

pedicels 15-30 mm (elongating in fruit), glabrous, flushed dark reddish-brown. ***Calyx*** tubular and somewhat inflated, membranaceous, pinkish or white, 15 mm long, lobes small, triangular, short-acuminate, 3-4 mm long, glabrous with a scattering of hairs on the apices of the lobes. ***Corolla*** creamy white or yellow, 25 mm long, very narrow, 3 mm wide at base and only widening slightly to the mouth, mouth strongly oblique, with lower lip elongated and strongly recurved, upper lobe oblong, c. 4 mm x 4 mm, lateral lobes also somewhat recurved, 4 mm x 3 mm, all lobes densely glandular hairy on inner surface, glabrous on outer surface. ***Stamens*** with filaments c 16 mm long, attached c 17 mm from base of corolla and extending beyond mouth of the corolla, glabrous; anthers 2–2.5 mm long, glabrous, connected at tips before dehiscence, staminodes 1–2 mm long, somewhat thickened at apex. ***Gynoecium*** 25 mm long; disc 1.5 mm, glabrous with an undulate margin; ovary glabrous; style glandular hairy for whole length; stigma peltate to somewhat bilobed, 2 mm across. ***Fruits*** broad-ovoid, almost sub-globose, glabrous, green (drying dark brown to black), 10–12 × 5–10 mm; calyx not or only partially persistent, base of style persistent.

Distribution. Central Sulawesi (Fig. 2.35).

Habitat and ecology. Lowland, hill and upland forest at an altitude of 300-1700 m.

Etymology. This species has been named for its long filaments that exceed the corolla.

Proposed IUCN conservation category. The EOO of this species is 10,876 km^2 and the AOO is 24 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). It has been collected from a wide altitudinal range from 300m on Gunung Dako to 1700m on Gunung Sojol in montane forest Cannon *et al*. (2007) which is one of the least threatened forest types in Sulawesi. As some of the collections were made within the Gunung Sojol National Park and Lore Lindu National Park (UNEP-WCMC & IUCN, 2019), a conservation assessment of Least Concern is proposed for this species.

Additional specimens examined. **Central Sulawesi.** Lore Lindu National Park, 400m N of Uwei Mboe, 17-26 vi 2011, *Brambach* 04-85 (CEB, E); Puncak Pinimoang, east of Kampung Sipatoh on the way to Gunung Sojol, 1153 m, 20 vii 2002, *Brown, Craven, Juswara & Ramadhanil* 83 (BO, CEB n.v., E); Lore Lindu National Park, vii-ix, 2006, *Culmsee* 425 (E, GOET); ibid, *Culmsee* 566 (E, GOET); Gunung Dako,

Teluk Bone, Lakatan, 300m, 24 ii 1985, *Ramlanto & Fanani* 509 (BO, L); Gunung Galang-Dako, 6 vii 2018, *Wahyudi Santoso & Rusdi* WS209 (BO).

Sulawesi Group: 8 (Atkins et al., Chapter 3).

Notes. This species is similar vegetatively to *C. fasciata, C. flavomaculata* and *C. kinhoii* in having decurrent leaves and tesselate stems. It is can be distinguished by its long pedicels (particularly in fruit), pale membranaceous calyx, and corolla with an elongated and recurved lower lobe with filaments and style extending beyond the mouth of the corolla. It is a variable species in terms of leaf size but all leaves have a distinctive narrow oblong shape. Three of the collections, including the type, are found in proximity to Gunung Sojol on the western end of the northern arm although over quite a wide altitudinal range. Three additional collections from Lore Lindu National Park in Central Sulawesi have been identified as this species as they have elongated pedicels, the remnants of a membranceous calyx and tesselate stems but they are difficult to place with certainty as the material is sterile.

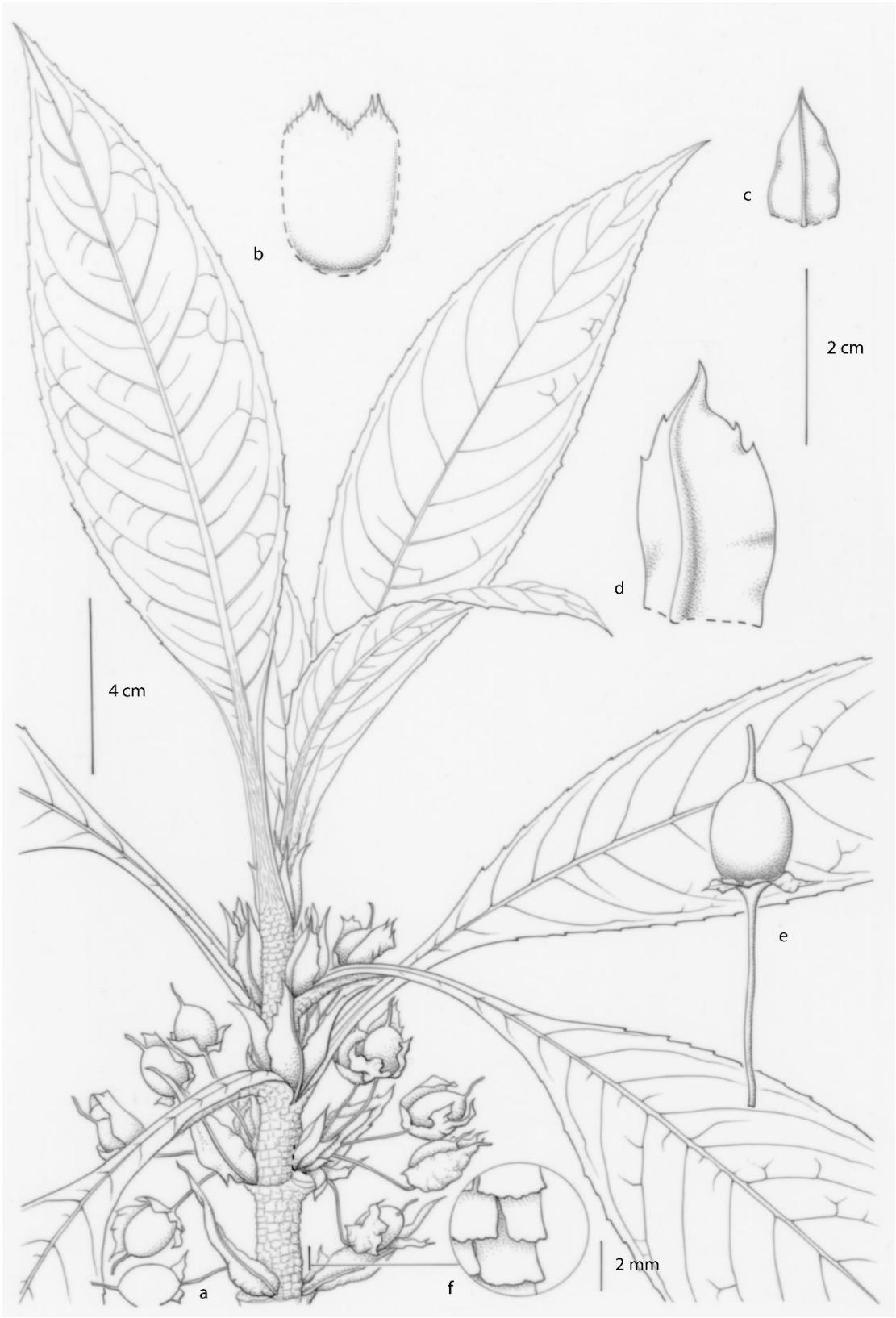


Fig. 2.34 Line illustration of *Cyrtandra longistamina* showing a.habit b. opened calyx showing inner surface c. bracteole d. bract e. fruit f. detail of tessellate stem surface. Drawn by Claire Banks from *Mendum* et al. 00197.

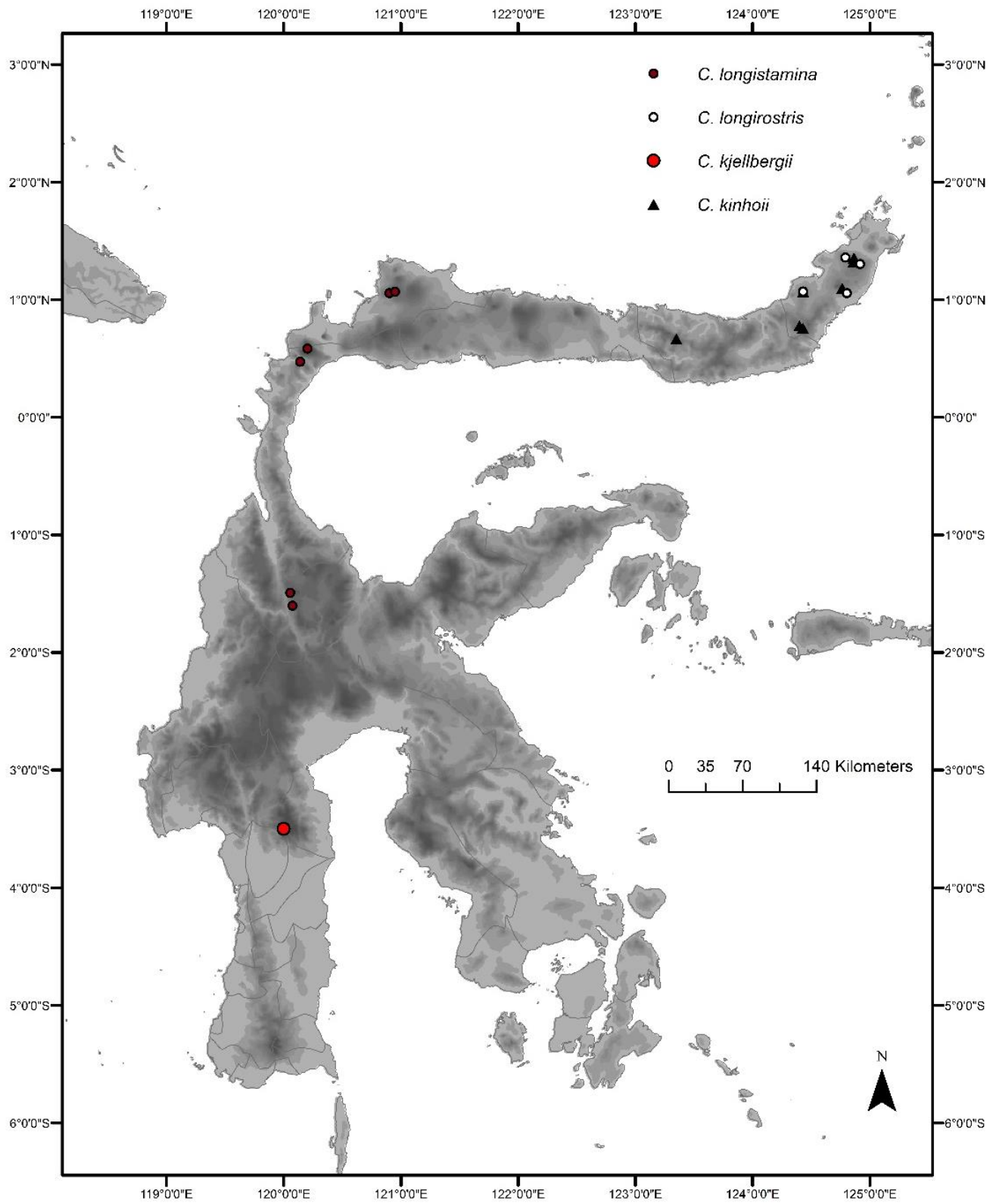


Fig. 2.35 Distribution of *Cyrtandra longistamina* (dark red circles), *C. longirostris* (white circles), *C. kjellbergii* (bright red circles) and *C. kinhoii* (black triangles).

Cyrtandra luteiflora H.J.Atkins, Edinburgh J. Bot. 60(3): 311 (2004) – Type: Sulawesi, Gorontalo, Gunung Gambuta, 10 iv 2002, *Atkins* et al. 52 (holotype BO, isotype E). **Fig. 2.36.**

Branching woody herb or ***shrub*** to 50 cm in height. ***Stems*** longitudinally striate, subglabrous, sparsely hairy when young. ***Leaves*** opposite; one of each pair markedly reduced or both well developed but somewhat unequal in size; petiole 5–8 mm long, sparsely hairy; blades of developed leaves 8.5–14 × 3.5–5 cm, narrowly obovate, occasionally somewhat rhomboid, apex acuminate, base acute, slightly asymmetric, shortly decurrent, margin with 3 or 4 distant, rounded narrow teeth or shallow lobes on each side; 4–5 pairs of lateral veins and some short side veins running to adjacent teeth, subglabrous above, sparsely hairy below, more densely so on midrib and veins. *Reduced leaves* 4 × 3 mm, either vestigial, cordate, or same shape as larger leaves. ***Inflorescences*** on trailing stems from base of main plant or subsessile in leaf axils; trailing stem c. 1 mm in diameter, up to 1.5 m long, glabrous, striate, dark green; bracts 3 × 1 mm, linear, sparsely hairy, not connate; pedicel 1–2 cm long, purple, sparsely hairy. ***Calyx*** purple, c. 15 mm long, slightly bilabiate with a deeper sinus between the three upper and two lower lobes, lobes c. 7 mm long, acuminate, glabrous to sparsely hairy, most densely so at apex of lobes. ***Corolla*** pale yellow with purple markings on lobes externally and two dark yellow to orange marks in throat, 40 mm long, narrowly funnel-shaped, arcuate, lower lobes 10 × 9 mm, upper lobes 8 × 8 mm, lobes spreading, sparsely hairy externally. ***Stamens*** with filaments 6 mm long, attached c. 25 mm above base of corolla, more or less glabrous with a scattering of short, glandular hairs near the anthers, white; anthers 1.5 mm long, cohering at apices, staminodes 3, laterals 2.5 mm long, central 1.5 mm long. ***Gynoecium*** 32 mm long; disc cupular, margin undulate, 2 mm long, glabrous; ovary glabrous; style white, glandular hairy; stigma white, peltate, 2 mm across. ***Fruits*** narrowly ovoid, dark brown, 15 × 4 mm, glabrous, calyx and base of style persistent.

Distribution: Gorontalo (Fig. 2.39).

Habitat and ecology. In upland forest at an altitude of 960m.

Etymology. This species was named for its distinctive, yellow flowers (Atkins, 2004).

Proposed IUCN conservation assessment. This species has only been collected from one locality on Gunung Gambuta and it is therefore not possible to calculate an EOO but the species has an AOO of 4 km^2 based on a 2 x 2 km grid (Bachman et al., 2011) (map in Appendix 2.1). The collection was from an altitue of 960 m in upland forest which is a habitat threatened in Sulawesi from intensive agriclture and urban expansion (Cannon et al., 2007). Gunung Gambuta is within the limits of the Bogani Nani Wartabone National Park (UNEP-WCMC & IUCN, 2019) and, as such, should receive some protection. This area is one of the most under-collected on the island and it is therefore also likely that additional populations of this species exist. Given its distribution within a protected area a category of Least Concern is suggested for this species.

Additional specimens examined: **Gorontalo.** Gunung Gambuta, 10 iv 2002, *Scott* 02-47, grown at RBGE as accession 20021194, vouchered as *Scott* 504 (E).

Sulawesi Group 12 (Atkins et al., Chapter Three).

Notes: This is one of four species from Sulawesi in which the flowers are borne on trailing stems that originate from the base of the plant that includes *C. hypogaea, C. geocarpa* and *C. rantemarioensis*. *Cyrtandra luteiflora* can be distinguished from the others by its often anisophyllous leaves, yellow flowers and glandular style.

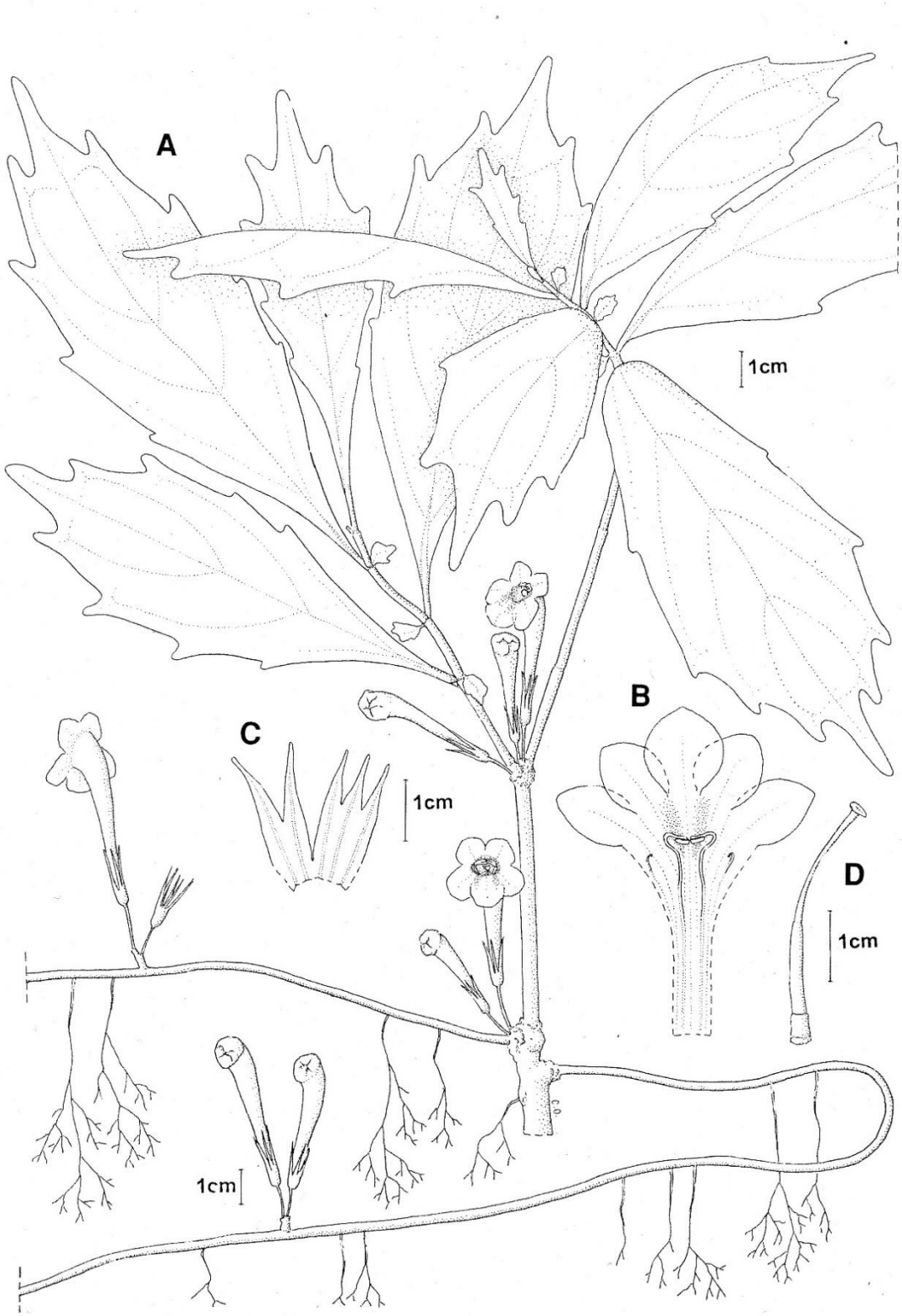


Fig. 2.36 Line illustration of *Cyrtandra luteiflora* H.J.Atkins showing a. Habit b. Opened corolla showing position of stamens and staminodes c. Opened calyx showing inner surface d. Gynoecium including disc. Drawn by Christina Oliver from *Atkins* et al. 52. Reproduced from Atkins (2004).

Cyrtandra mollis de Vriese, Pl. Ind. Bat. Orient*.:* 16 (1856). – *Rhynchocarpus mollis* Reinw. ex de Vriese, Pl. Ind. Bat. Orient*.* 16 (1856), nom.nud. – Type: Celebes [Sulawesi], in sylva montosa, x 1821, *Reinwardt* 1546 (lectotype L hic. desig.).

Cyrtandra vriesii C.B.Clarke syn. nov., A. & C.DC., Monogr. Phan*.* 5: 237 (1883). Type. Celebes [Sulawesi], Minahassa, 1 vii 1859, *de Vriese & Teijsmann* 24 (lectotype L hic desig.). **Fig. 2.37**

Shrub to 4 m in height. ***Stems*** striate, hairy, densely so on young growth. ***Leaves*** opposite; sometimes in threes, those of a group or pair well developed but somewhat unequal in size; petiole 15–20(–50) mm long, hairy to densely hairy; blades 6–18 (–30) cm × 3–6(–10) cm, elliptic to narrow elliptic, sometimes lanceolate, apex acuminate, base acute, briefly decurrent, slightly asymmetrical, margin serrulate; 10–12 pairs of lateral veins, curving upwards and running out to margin, hairy to densely hairy above and below including midrib and veins. ***Inflorescences*** axillary, subsessile, 1–2-flowered; bracts 10-15 mm long, linear, densely hairy, soon caducous; pedicel 4–5 mm long, densely hairy. ***Calyx*** pale green, flushed reddish on lobes to deep red throughout, 12–16 mm long, more or less evenly divided, lobes long-acuminate, 8–10 mm long, or sometimes with lobes strongly adpressed, hairy. ***Corolla*** flushed reddish-pink along tube, lobes pale yellow with pale guidemarks, 27–38 mm long, tubular, gradually widening to mouth, slightly arcuate, lower and lateral lobes oblong, strongly recurved, 7 mm x 6 mm, upper lobe oblong, erect or extending forwards, 6-7 mm × 4.5–5 mm, mouth oblique, glandular hairy externally and internally on lobes and base of tube. ***Stamens*** with filaments 10–15 mm long, attached 14–15 mm from base of corolla, orange brown, glabrous, slightly glandular towards the anthers; anthers brownish, 1.5–2.5 mm long; staminodes 3, lateral staminodes 3–6 mm long, central staminode less than 1 mm long. ***Gynoecium*** 20–32 mm long; disc cupular with undulate margin, 1 mm long, glabrous; ovary subglabrous, style glandular-hairy; stigma peltate, slightly bilobed, 2.5 mm across, exserted from mouth of corolla at maturity. ***Fruits*** narrow ovoid to oblong, glabrous except for glandular hairy persistent style, 20–25 mm × 5 mm, calyx and style persistent.

Distribution. North Sulawesi (Fig. 2.39).

Habitat and ecology. Upland forest at an altitude of 1100-1400 m.

Etymology. The epithet 'mollis' means soft or pliant and possibly refers to the soft indumentum which is velvety to the touch or to the soft texture of the leaves.

Proposed IUCN conservation category. This species has an EOO of 1,014 km^2 and an AOO of 32 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). Two of the collections are from within the Gunung Ambang Nature Reserve and should receive some protection (UNEP-WCMC & IUCN, 2019) but most are from the more densely populated areas around Manado and Tomohon where there is pressure from urban expansion and intensive agriculture on upland forest (Cannon et al., 2007). Given the restricted distribution of this species and the lack of formal protection across most of its distribution in an area of high population density, this species is considered to be Vulnerable under the VUD2 category.

Additional specimens examined: **North Sulawesi**. Gunung Ambang Nature Reserve, near Singsingon village, 2 xi 2016, *Barber, Atkins, Kartonegoro* & *Kinho* BAKK42 (BO, E); Gunung Ambang accessed from Bongkudai Baru village, 3 xi 2016, *Barber, Atkins, Kartonegoro* & *Kinho* BAKK52 (BO, E); Gunung Mahawu, 6 xi 2016, *Barber, Atkins, Kartonegoro* & *Kinho* BAKK83 (BO, E); Wagio crater, Mt Mahawae, Tomohon, 4 vii 1956, *Forman* 395 (BO, K, L); Menado, Beclang, *HB* 5343 (BO, L); Menado, *HB* 5362 (BO); Minahassa, 5 v 1895, *Koorders* 17181 (BO, L); 7 i 1859, *Koorders* 17194 (BO, L); Tondano, 1923, *Kruyff* 17 (BO), Mt Soputan, 11 x 1973, *de Vogel* 2498 (A, CANB, L); Minahassa, 1 vii 1859, *de Vriese & Teysmann* 24 (L).

Sulawesi Group 13 (Atkins et al., Chapter Three).

Notes. This species is the most densely hairy of the Sulawesi species and is reminiscent, in this sense, of *C. villosissima* Merrill from Mindanao and *C. hirtigera* H.J.Atkins & Cronk from Palawan. The corolla is unusual in Sulawesi with its pale yellow and pink colouring, which appears almost metallic, and the recurved upper lobes. Collections of *C. mollis* from the same population on Gunung Ambang (*Barber* et al. BAKK42 and BAKK52) showed significant variation in the colour of the stems, leaves and calyces from light green to deep red.

Cyrtandra vriesii C.B.Clarke has been reduced to synonymy here for the first time, following the herbarium annotations of B.L.Burtt. De Vriese cited a Reinwardt collection from 1821 'in sylva tomentosa insulae Celebes' and the manuscript name and number *Rhynchocarpus mollis* mss no

1546 when he described *C. mollis*. The Leiden specimen matching these details (L0277511) is selected here as the Lectotype of *C. mollis*. Clarke (1883) listed *De Vriese & Teysmann* 24 in the Leiden herbarium after his description of *C. vriesii* and that specimen is selected here as the Lectotype for that name.

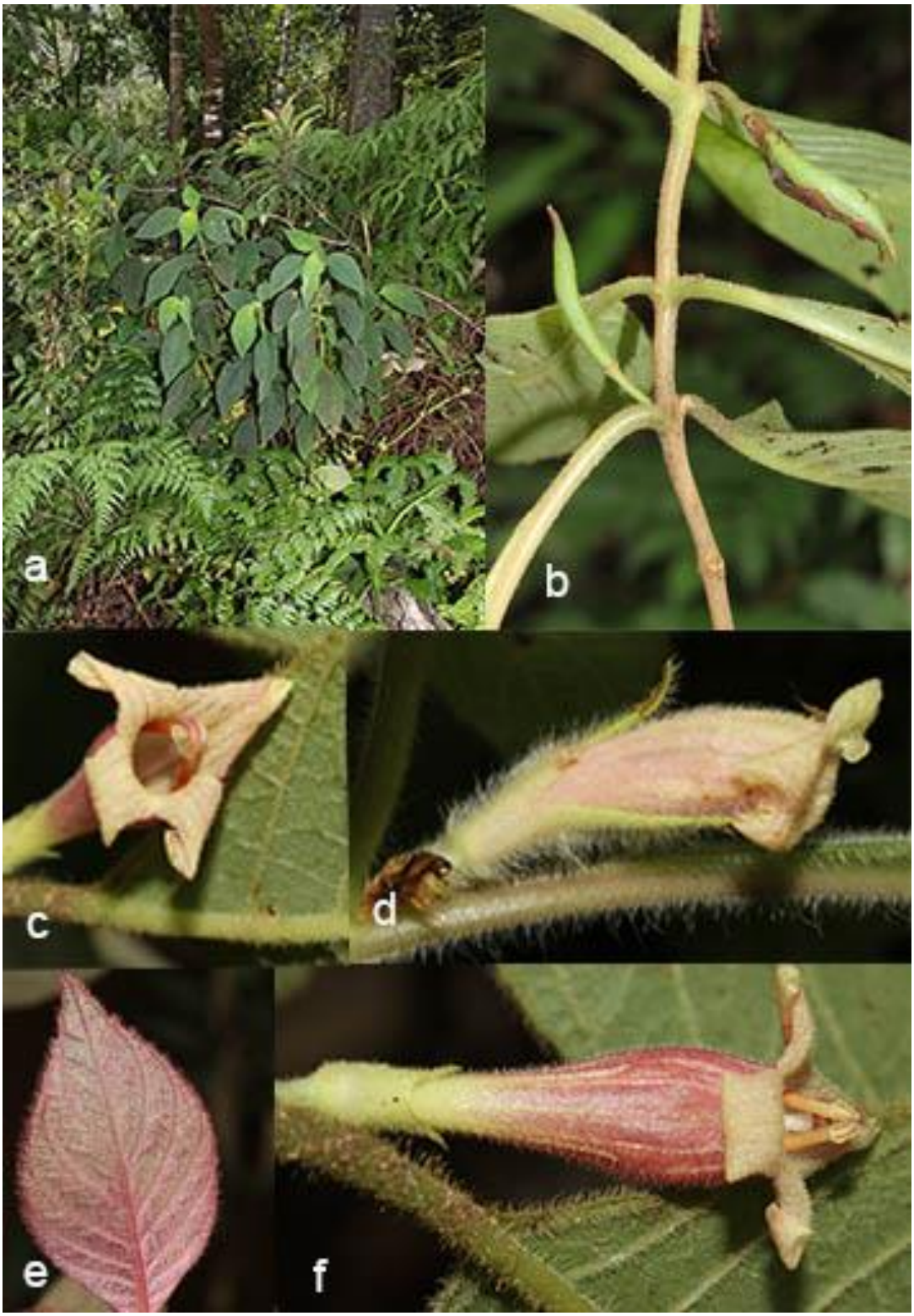


Fig. 2.37 Plate of *Cyrtandra mollis* showing a. habit b. fruits c. front view of flower d. side view of corolla e. leaf under surface showing reddish colouring on some plants f. view of corolla from below. Photos: Sadie Barber. BAKK42 and BAKK52.

Cyrtandra multinervis Karton. & R.Bone, Edinburgh J. Bot. 75(2): 21 (2018) – Type: Sulawesi, Tongoa, Mt Potong, 8 iii 2001, *Kessler, P.J.A.* et al. PK 2974 (holotype BO; isotypes E, K, L). **Fig. 2.38**

Branching shrub to 4 m in height. ***Stems*** ridged, striate, glabrous. ***Leaves*** opposite, subequal; petioles 4–5 cm long, glabrous; blades up to 31 x 9.5 cm, oblong or narrow-elliptic, apex acuminate, base attenuate, somewhat oblique, margin subentire to minutely and distantly crenulate; 17–19 pairs of lateral veins and faint, reticulate tertiary venation, dark green and glabrous above, paler green and glabrous below. ***Inflorescences*** axillary, 1–5-flowered; peduncle 15–18 mm long, glabrous; bracts 20–23 x 9–12 mm, enclosing the flowers when in bud, ovate, glabrous; bracteoles, 9–11 x 3–4 mm, ovate-elliptic, glabrous; pedicels 6–8 mm long, glabrous. ***Calyx*** tubular, pale green, 16–18 mm long, glabrous, lower lobes acuminate, 7–8 mm long, upper lobes, 3–4 mm long. ***Corolla*** white with red in the throat, 18–23 mm long, glabrous, lobes recurved, just showing above the top of the calyx, upper lobes rounded, c. 6 x 4 mm, lower and lateral lobes rounded, c. 4 x 3 mm. ***Stamens*** with filaments 5–7 mm long, attached c. 9–10 mm above the base of the corolla, glabrous; anthers c. 2 mm, cohering at apices. ***Gynoecium*** c. 15 mm long; disc cupular c. 1 mm long, glabrous; ovary glabrous; style glabrous at base, short hairy at apex; stigma bilobed, c. 1 mm across. ***Fruits*** oblong, narrow, sometimes curved, drying black, (10–)17–25 x 1–2 mm, glabrous, smooth; base of style persistent, calyx not persistent.

Distribution: Central Sulawesi, known only from the type locality in Tongoa. Fig. 2.39.

Habitat and ecology. Upland forest at an altitude of c. 980 m.

Etymology. Named for the high number of lateral veins on the leaf blades (Kartonegoro et al., 2018).

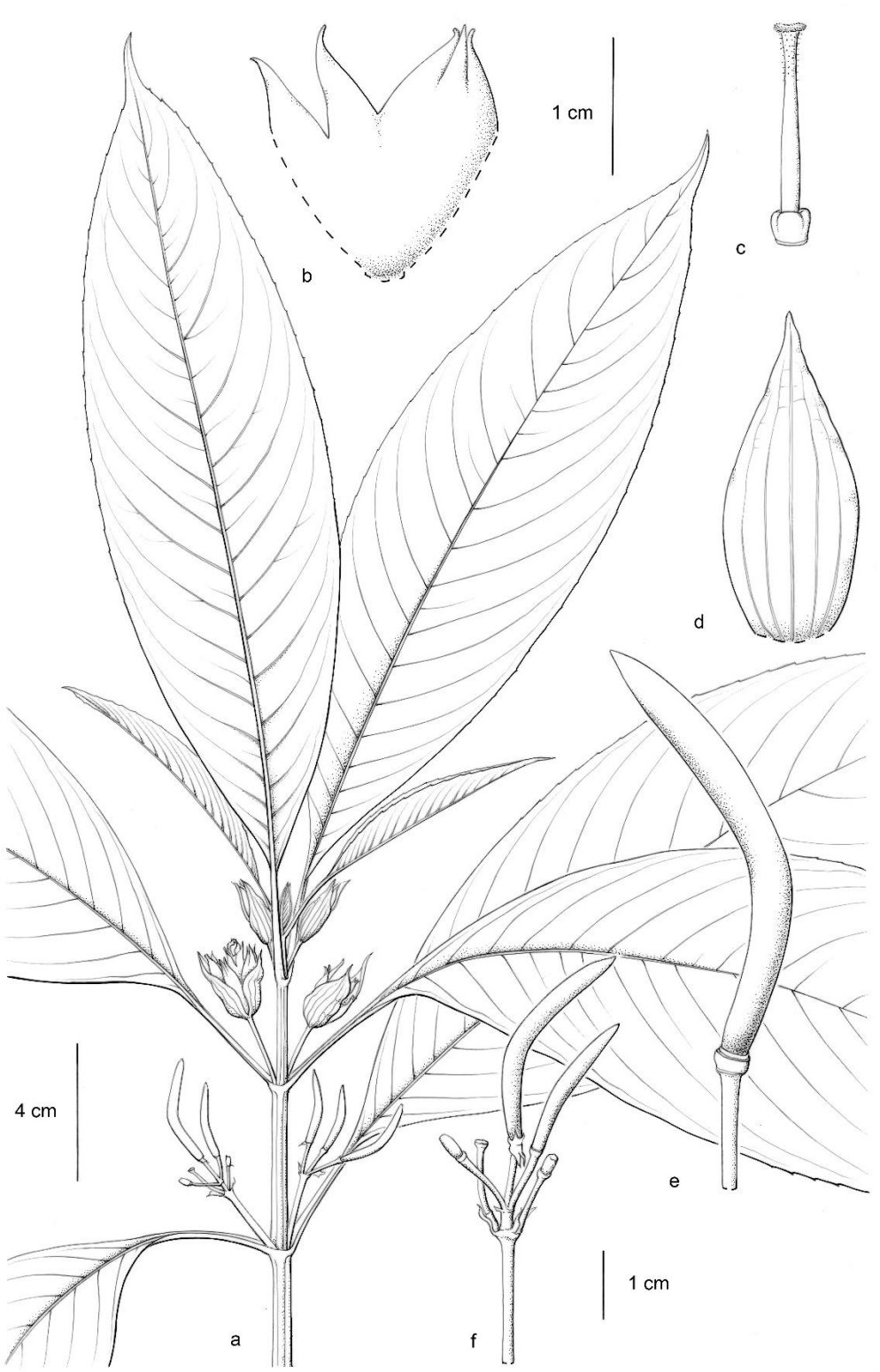


Fig. 2.38 Line illustration of *Cyrtandra multinervis* showing a. Habit b. Opened calyx showing inner surface c. Gynoecium showing disc d. Bract e. Fruit.f. Infructescence. Drawn by Claire Banks from *Kessler* et al. PK 2974. Reproduced from Kartonegoro et al. (2018).

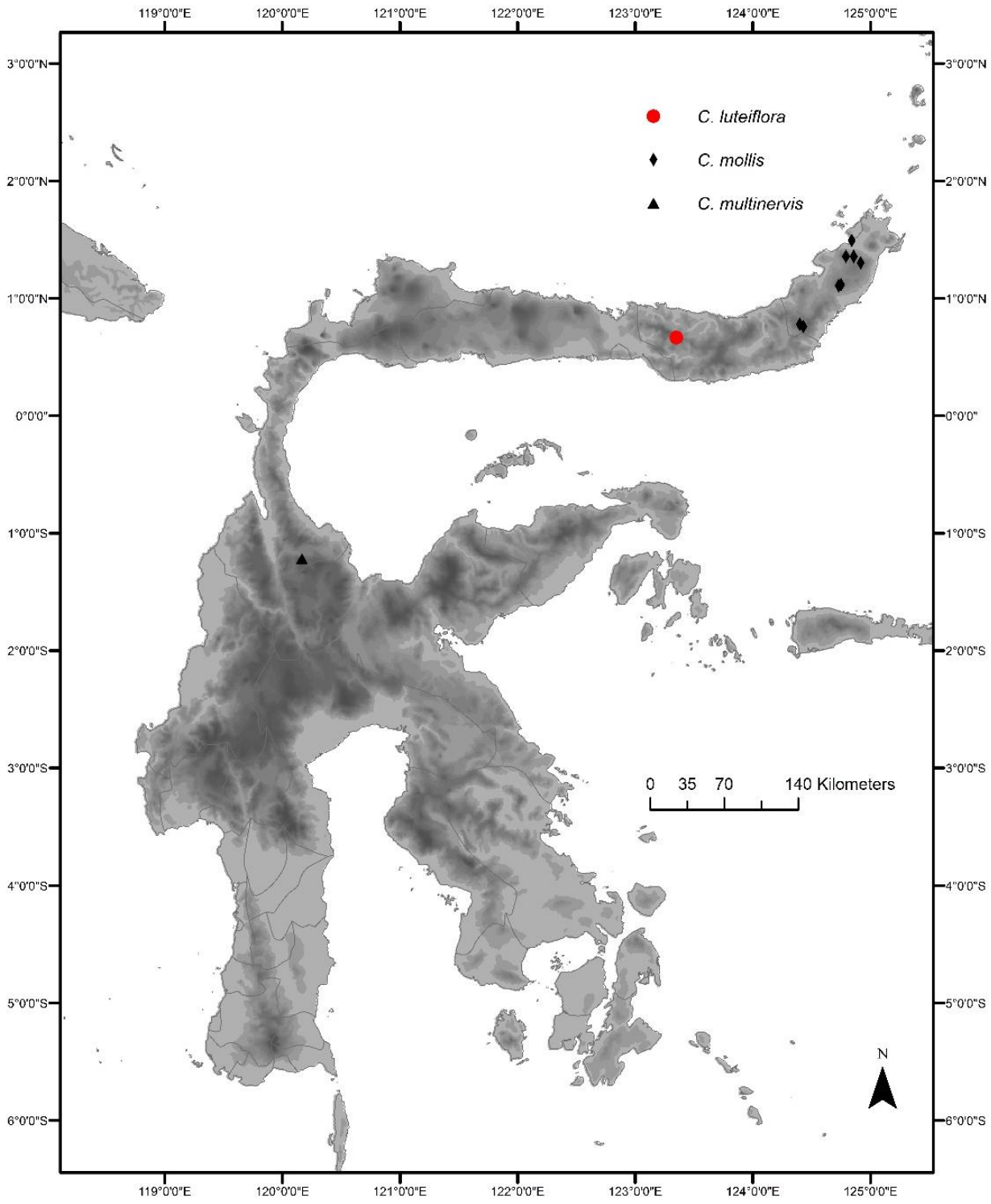


Fig. 2.39 Distribution of *Cyrtandra luteiflora* (red circles)*, C. mollis* (black diamonds) and *C. multinervis* (black triangles).

Proposed IUCN conservation category. It has not been possible to calculate EOO as there is only one collection for this species but the AOO is 4 km^2 based on a 2 x 2 km cell (Bachman et al., 2011) (map in Appendix 2.1). This collection falls within the limits of the Lore Lindu National Park (a UNESCO Biosphere Reserve) and as such will have some protection (UNEP-WCMC & IUCN, 2019). It has only been collected once from a relatively well collected area of Sulawesi, suggesting it is probably not locally abundant. It was collected in upland forest which is one of the more threatened habitats in Sulawesi (Cannon et al., 2007). It is suggested a category of Vulnerable is given for this species under the category VUD2 to reflect the low number of collections and the known threats to this habitat type (Cannon et al., 2007).

Additional specimens examined. This species is known only from the type collection.

Sulawesi Group 6 (Atkins et al., Chapter Three).

Notes. This species has been described from a single collection but is very distinctive in Sulawesi due to its narrow fruits and many nerved leaves.

Cyrtandra nitida Karton. & H.J.Atkins**,** Edinburgh J. Bot. 75(2): 24 (2018) – Type: Sulawesi, North of Mangkutana, Wotu to Lake Poso road, 20 ii 2000, *Mendum, Argent & Hendrian* 00111 (holotype BO; isotype E, CEB). **Fig. 2.40**

Herb to 2 m in height, sometimes branching from the base. ***Stems*** longitudinally ridged, flushed purple, sparsely woolly–hairy, more densely so on young growth. ***Leaves*** opposite, unequal, both well developed; blades 15.5–30.5 x 4.5–9 cm, oblong to narrowly oblong, apex acuminate, base attenuate becoming auriculate, clasping the stem and touching the base of the opposite leaf, margin serrulate; 11–15 pairs of lateral veins, tertiary venation obscure; dark glossy green turning almost white at the base, more or less glabrous with some scattered hairs above; much paler below with a sparse covering of fine, golden hairs, more densely so on the mid rib and veins. ***Inflorescences*** axillary, tucked in to the auriculate leaf bases, with c. 10–12 flowers at various stages of development; single bract green, 15–22 x 5–8 mm, lanceolate-ovate, apex acuminate, margin slightly serrate, densely hairy above, less so below, caducous; bracteoles lanceolate, green, 15–20 x 4–5

mm; pedicels light green, 3–5 mm long, hairy. ***Calyx*** green, 7–8 mm long, more or less evenly 5–lobed, lobes divided almost half way to the base, 3– 4 mm, acuminate, sparsely hairy, more densely so on lobes. ***Corolla*** white, 8–12 mm long, tube narrow, lobes spreading, slightly projecting forwards, upper and lateral lobes orbicular, c. 5 x 4 mm, lower lobe slightly longer and ovate, c. 6 x 4 mm, subglabrous externally, with a dense covering of short, glandular hairs internally on the lobes and the mouth of the tube. ***Stamens*** with filaments 1–2 mm long, attached c. 4 mm from the base of the corolla, glabrous; anthers 1 mm long, glabrous; staminodes 3, c. 0.5 mm long. ***Gynoecium*** 4–6 mm long; disc cupular with undulate margin, c. 1 mm long, glabrous; ovary glabrous at base; style glandular hairy towards apex; stigma bilobed, lobes vertical, 0.8–1 mm across. ***Fruits*** ovoid, dark green, brown and verrucose when dry, 4–5 x 2–3 mm; most of calyx and base of style persistent.

Distribution. Central and South Sulawesi, close to the border of both provinces (Fig. 2.42).

Habitat and ecology. Steep, rocky roadside banks in hill and upland forest at an altitude of 500–1255 m.

Etymology. This species is named for its distinctive glossy leaves (Kartonegoro et al., 2018).

Proposed IUCN conservation category. It has not been possible to calculate the EOO for this species as the exact locality of two of the collections is not known but it has an AOO of 8 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011). The species has been collected in hill and upland forest between 500 and 1255 m in relatively disturbed areas without formal protection (UNEP-WCMC & IUCN, 2019). Following Kartonegoro et al., (2018) a category of Vulnerable under the VUD2 criteria is suggested for this species to reflect its restricted distribution and occurrence in relatively disturbed areas without formal protection (UNEP-WCMC & IUCN, 2019).

Additional specimens examined. **Central Sulawesi.** Gunung Mad, Pegunungan Biru, Poso-Napu road divide, 3 viii 2018, *Ardi* WI291 (KRB);

South Sulawesi: 21 km south of border line between S. Sulawesi and C. Sulawesi, 12 xii 1994, *Sidiyasa 1369* (K, L).

Sulawesi Group 5 (Atkins et al., Chapter Three).

Notes. This species is very distinctive and unlike any others in Sulawesi due to its glossy upper leaf surface and the auriculate leaf bases which clasp the stem and hold the inflorescence.

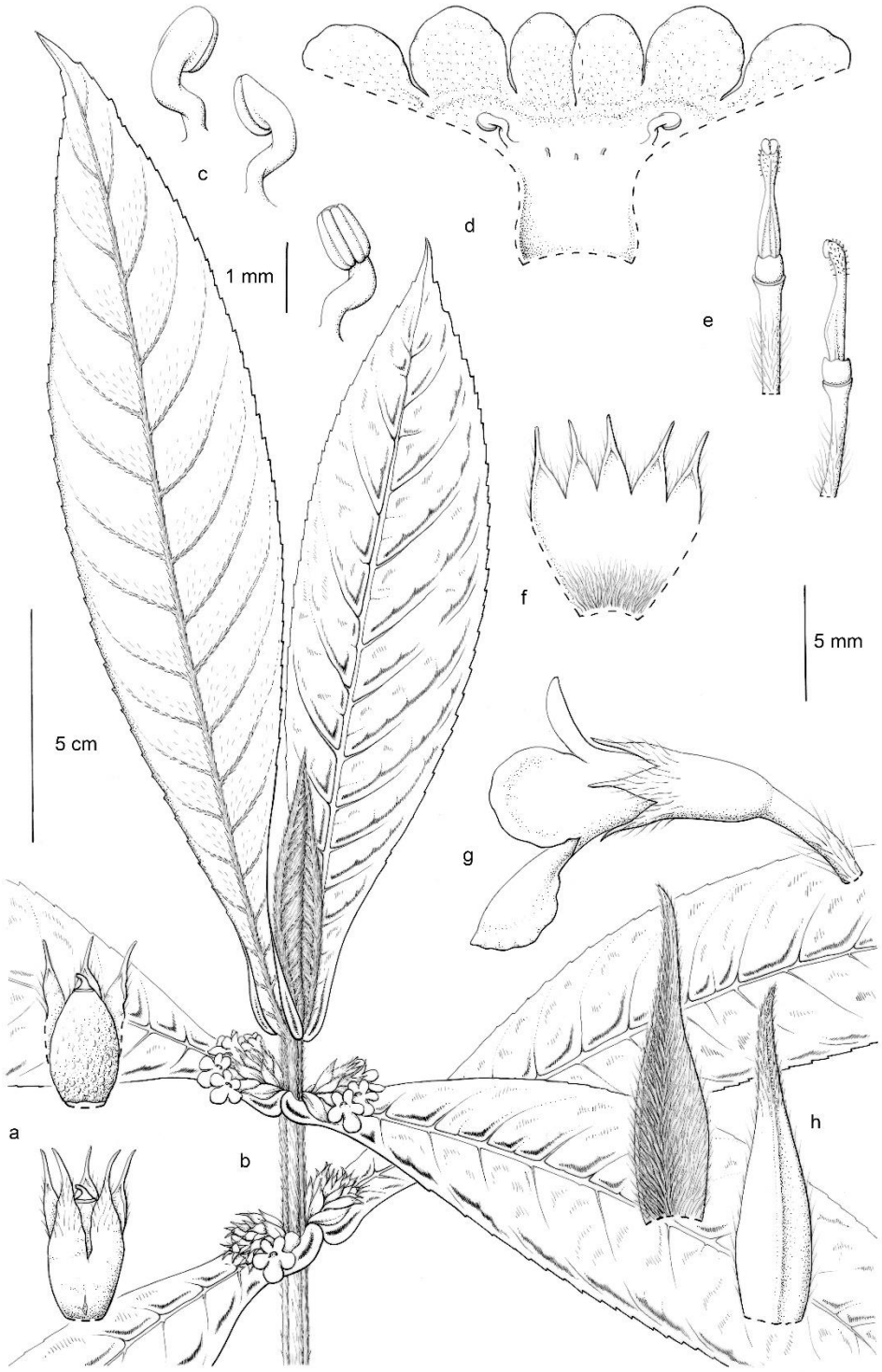


Fig. 2.40 Line illustration of *Cyrtandra nitida* showing a. Fruit with and without calyx b. Habit c. Anthers d. Opened corolla showing position of stamens and staminodes e. Front and side view of gynoecium including pedicel f. Opened calyx g. Side view of corolla h. Internal and external view of bracts. Drawn by Claire Banks. Habit and fruit drawn from *Sidiyasa* 1369. Flowers from *Mendum* et al. 00111. Reproduced from Kartonegoro et al. (2018).

Cyrtandra parvicalyx H.J.Atkins & Karton. **sp. nov.** ined.

Similar to *C. sopuensis* in having markedly anisophyllous leaves, white, hairy flowers and hairy fruits but distinguished by its fewer and much smaller, caducous inflorescence bracts (bracts 2–3 mm long, caducous in *C. parvicalyx* vs 6–10 mm long, persistent in *C. sopuensis*); smaller leaves with fewer pairs of lateral leaf veins (leaves 6-9 cm x 1.5-2.5 cm with 4–5 pairs of lateral veins in *C. parvicalyx* vs leaves 11-13 cm x 3-3.5 cm with 7–12 pairs of lateral veins in *C. sopuensis*) and longer pedicels (4–7 mm long in *C. parvicalyx* vs 2–3 mm long in *C. sopuensis*).-Type: Central Sulawesi, Gunung Sojol, 26 ii 2000, *Mendum* et al. 00158 (holotype E; isotype BO).

Shrub to 1m in height. ***Stems*** striate, subglabrous, hairy on young growth. ***Leaves*** usually appearing alternate, sometimes opposite with one leaf of a pair markedly reduced; petioles 8–10 mm long, glabrous to sparsely hairy; blades 6–9 cm × 1.5–2.5 cm, oblanceolate, apex long acuminate, base acute, not decurrent, slightly asymmetrical, margin subentire to serrulate; 5 pairs of lateral veins, curving upwards and eventually out to margin; subglabrous above, sparsely hairy below more densely so on midrib and veins. *Reduced leaves* (where present) cordate, 2 mm × 1 mm. ***Inflorescences*** axillary, sessile, 1–2(–3)-flowered; bracts linear, 2–3 mm × 1 mm, hairy, caducous; pedicels 4–7 mm long, hairy. ***Calyx*** cupular, evenly 5-lobed, white, 3–5 mm long , 1/4 to 1/3 corolla length, lobes narrow, acuminate at apex, 2–3 mm, hairy externally. ***Corolla*** white, 12–16 mm long , narrow funnel-shaped, narrow in basal half then gradually widening to mouth, lobes spreading, upper lobes rounded, somewhat acute at apex, 3–4 mm × 2–2.5 mm, lower and lateral lobes oblong, acute at apex 3–4 mm × 2–3 mm, long white hairy externally. ***Stamens*** with filaments 4–5 mm long, attached 7–8 mm from the base of corolla, glabrous*;* anthers 0.8–1 mm long, connected at tips before dehiscence; staminodes 3, 0.5 mm long. ***Gynoecium*** 10–14 mm long; disc cupular with deeply lobed margin, 1–1.5 mm long, glabrous externally but with a fringe of hairs along margin; ovary and style densely eglandular hairy; stigma bilobed, 1–1.2 mm across. ***Fruits*** narrow ovoid, 10 mm × 3 mm (excluding style), densely hairy; style persistent, calyx not persistent.

Distribution: Central Sulawesi: Gunung Sojol (Fig. 2.42).

Habitat and ecology. Upland forest at an altitude of c. 1400m.

Etymology. Named after its short calyx relative to the length of the corolla.

*Proposed IUCN conservation category.*This species is only known from the Type location so it has not been possible to calculate the EOO but it has an AOO of 4 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). It was collected in the Gunung Sojol Nature Reserve (UNEP-WCMC & IUCN, 2019) from an altitude of c. 1400 m close to the edge of montane forest *sensu* Cannon *et al*. (2007) which is one of the less threatened forest types in Sulawesi (70% of upland forests above 1500m elevation are intact). Despite the very restricted distribution of this species, a category of Least Concern is suggested due to its location in a protected area and in a relatively unthreatened habitat.

Additional specimens examined. This species is only known from the type collection.

Sulawesi Group 14 (Atkins et al., Chapter Three).

Notes. This species is part of a group on the island that share the characteristics of markedly anisophyllous leaves, white, hairy flowers and hairy fruits. It can be most easily distinguished from the others in the group by a combination of its short calyx relative to the length of the corolla, cordate reduced leaves and its very narrow, tubular corolla only widening near the mouth.

Cyrtandra polyneura (C.B.Clarke) B.L. Burtt, Edinburgh J.Bot. 47(3): 225 (1990). – *Cyrtandra decurrens* de Vriese var. *polyneura* C.B.Clarke, A. & C. DC., Mon. Phan. 5: 233 (1883). – Type: Celebes [Sulawesi], Minahassa, Tondano, iv. 1840, *Forsten* 86 (holotype L). **Fig. 2.41**

Herb or ***shrub*** to 1 m in height. ***Stems*** striate, sparsely hairy, more densely so on young growth. ***Leaves*** opposite; those of a pair subequal or well developed but somewhat unequal in size; blades 15–35 cm × 5–10 cm, oblanceolate, apex short-acuminate, base decurrent, laminas of opposite leaves connate at base when young, margin serrate; 7–15 pairs of lateral veins, curving upwards and running out to margin, glabrous above, often warty at base, sparsely hairy below, more densely so on midrib and veins. ***Inflorescences*** axillary, subsessile or pedunculate, many-flowered; bracts up to 25 mm × 20 mm, subglabrous, warty at base, partially united, forming an involucre containing 8–16(–20) small flowers at various stages of development; peduncles up to 25 mm long, hairy; pedicels 1–3 mm long, glabrous to sparsely hairy, sometimes warty. ***Calyx*** tubular, greenish-brown, 8–9 mm long, sparsely hairy, 5-lobed, lobes acuminate at apex, 2–3 mm long. ***Corolla*** white to pale yellow with yellow or pale orange patches on lobes and throat and red spots in throat, 10–15 mm long, tube narrow in basal third, gradually widening to mouth in apical two thirds, lobes not recurved, upper lobes 2–3 mm × 3 mm, lower lobes 3 mm × 4 mm, hairy externally, and with a scattering of glands below the lobes internally. ***Stamens*** with filaments 3–5 mm long, attached 5 mm from base of corolla, glabrous but with some sessile glands; anthers 1–1.5 mm long, face to face and connected at apices before dehiscence; staminodes 3, laterals c. 4 mm long, central 1.5 mm long. ***Gynoecium*** 10 mm long; disc 1–1.5 mm long, cupular with lobed margin, glabrous; ovary subglabrous to sparsely eglandular hairy; style eglandular hairy for whole length; stigma peltate, slightly bilobed, 1.5–2 mm across. ***Fruits*** narrow ovoid to oblong, green or turning purplish, up to 10 mm × 5 mm, subglabrous; calyx and bracts not persistent.

Distribution. North Sulawesi, Gorontalo, Central Sulawesi, South Sulawesi, South East Sulawesi, West Sulawesi (Fig. 2.42).

Habitat and ecology. Disturbed lowland, hill and upland forest at an altitude of 200-1200 m.

Proposed IUCN conservation category. This is one of the most common and widespread species on the island and, unusally for *Cyrtandra,* is often found growing in large patches. The EOO for this

species is 294,062 km^2 and the AOO is 132 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). We propose a category of Least Concern for this species.

Additional specimens examined: **North Sulawesi**. Minahassa, W. slope of Mt. Masarang, 20 vi 1954, *Alston* 15952 (A, BM, BO); Tanggari, 5 vii 1954, *Alston* 16223 (BM); G. Manembo-nembo, 28 vii 1954, *Alston* 16576 (A, BM, BO); Gunung Masarang, 2 ii 2019, *Ardi* WI398 (KRB); Bolaang Mongondow, Kasingolan River, 30 x 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK18 (BO, E); Gunung Ambang Nature Reserve, 2 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK41 (BO, E); Manado, 4 iii 1895, *Koorders* 17109B (BO); Mt Masarang, 10 i 1895, *Koorders* 17185 (BO); Minahasa, 4 iii 1895, *Koorders* 17189B (BO,L); Kajoewatoe, 23 ii 1895, *Koorders* 17195 (BO, L); Gunung Klabat, 19 i 1895, *Koorders* 17200B (BO); Sangihe Talaud, Talaud, s slope of G. Duata, 30 iv 1926, *Lam* 2697 (S);

Gorontalo. Gorontalo, route along the Olama river to Gunung Gambuta, 9 iv 2002, *Atkins* et al. 40 (BO, E); Between Pinogu and Tulabolu, 15 iv 2002, *Atkins* et al. 114 (E, BO); Path from Bululi to Gunung Boliohutu, 22 iv 2002, *Atkins* et al. 142 (BO, E); Gunung Boliohutu, 22 iv 2002, *Scott* 02-106, grown on at RBGE as accession 20141650, vouchered as *Atkins* 58 (E);

Central Sulawesi. Gunung Nokilalaki, 24 ii 2018, *Ardi* WI220 (KRB); Gunung Mad, 3 viii 2018, *Ardi* WI288 (KRB); Lore Lindu National Park, Tamping Lake area, 4 viii 2018, *Ardi* WI300 (KRB); Sopu Valley, c 80 km SSE of Palu, 26 iv 1979, *van Balgooy* 3005 (A, E, L); Luwuk area, inland from Batui, 14 x 1989, *Coode* 5933 (BO, K, L); G. Loemoet, Biv.V-Biv.I, 7 ix 1938, *Eyma* 3697 (BO); East of Tongoa, 2 iii 1981, *Johansson, Nybom* et al. 135 (E, L); Mt Sojol, 29 ii 2000, *Mendum* et al. 00217 (E); Luwuk, Hanga-Hanga waterfall, 8 iv 2008, *Thomas & Ardi* 08-25 (BO, E); steep river bank, 24 iv 2008, *Thomas & Ardi* 08-63 (BO); steep river bank, 24 iv 2008, *Thomas & Ardi* 08-64 (BO, E); between rocks on riverside, 24 iv 2008, *Thomas & Ardi* 08-65 (BO, E); Gunung Galang-Dako, 8 vii 2018, *Wahyudi Santoso Rusdi* WS256 (BO);

South Sulawesi. Soroako-Wasuponda Road, 7 vii 1979, *van Balgooy* 3911 (A, BO, E, L);

South East Sulawesi. Kolaka, Mt Pondunaah, 13 v 2008, *Girmansyah* 883 (BO); Mt Watuwila village of Sanggona, 15 v 2008, *Kartonegoro* ARK239 (BO); Tinukari Village, 29 vi 2010, *Widjaja & Sujadi* EAW9051 (BO, E); ibid., 30 vi 2010, *Widjaja, Sujadi, Santoso & Hapid* EAW9699 (BO); ibid, 30 vi 2010, *Widjaja, Sujadi, Santoso & Hapid* EAW9712 (BO); Gunung Watuwila, 17 v 2008, *Wiriadinata* HW13371 (BO);

West Sulawesi. Tapalang, 4 viii 1912, *Noerkas* 433 (BO, L).

Sulawesi Group 2 (Atkins et al., Chapter Three).

Notes. This is one of the most widespread and common species in Sulawesi, distinguished by its involucrate, many-flowered axillary inflorescences and decurrent leaves.

This species was originally described as a variety of the Moluccan species *C. decurrens* de Vriese by C.B.Clarke (1883). It was subsequently raised to species level by Burtt (1990), the Sulawesi species being distinguished by having much longer leaves; warty, partially united inflorescence bracts and sparsely hairy calyx lobes (Burtt, 1990).

A number of the specimens record that the plant is collected and eaten as a vegetable.

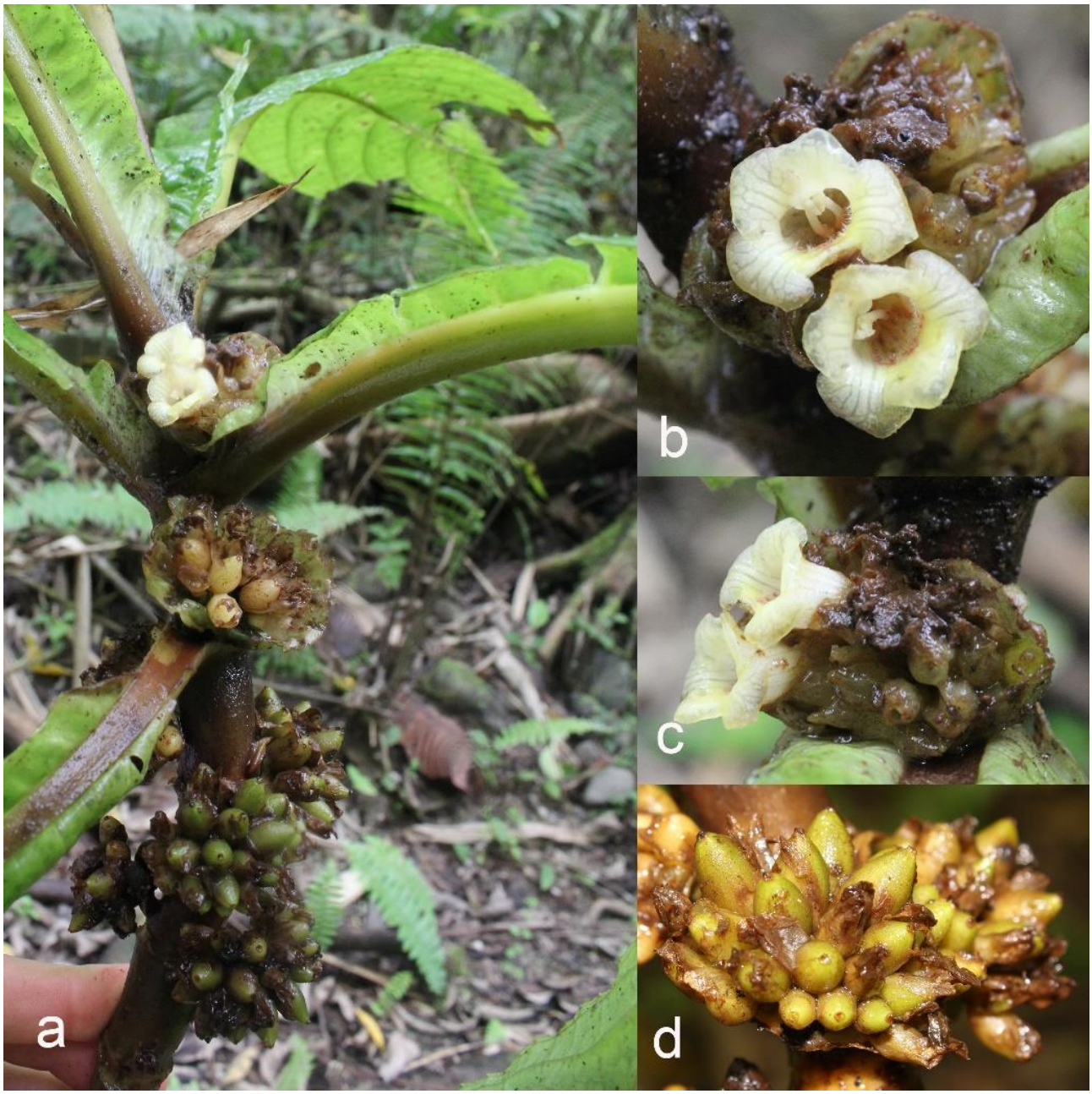


Fig. 2.41 Plate of *Cyrtandra polyneura* showing a. habit and stem showing inflorescences and infrutescence at various stages b. front view of corolla and bracts forming an involucre c. side view of flower and young buds d. fruits. Photos: Sadie Barber. BAKK18.

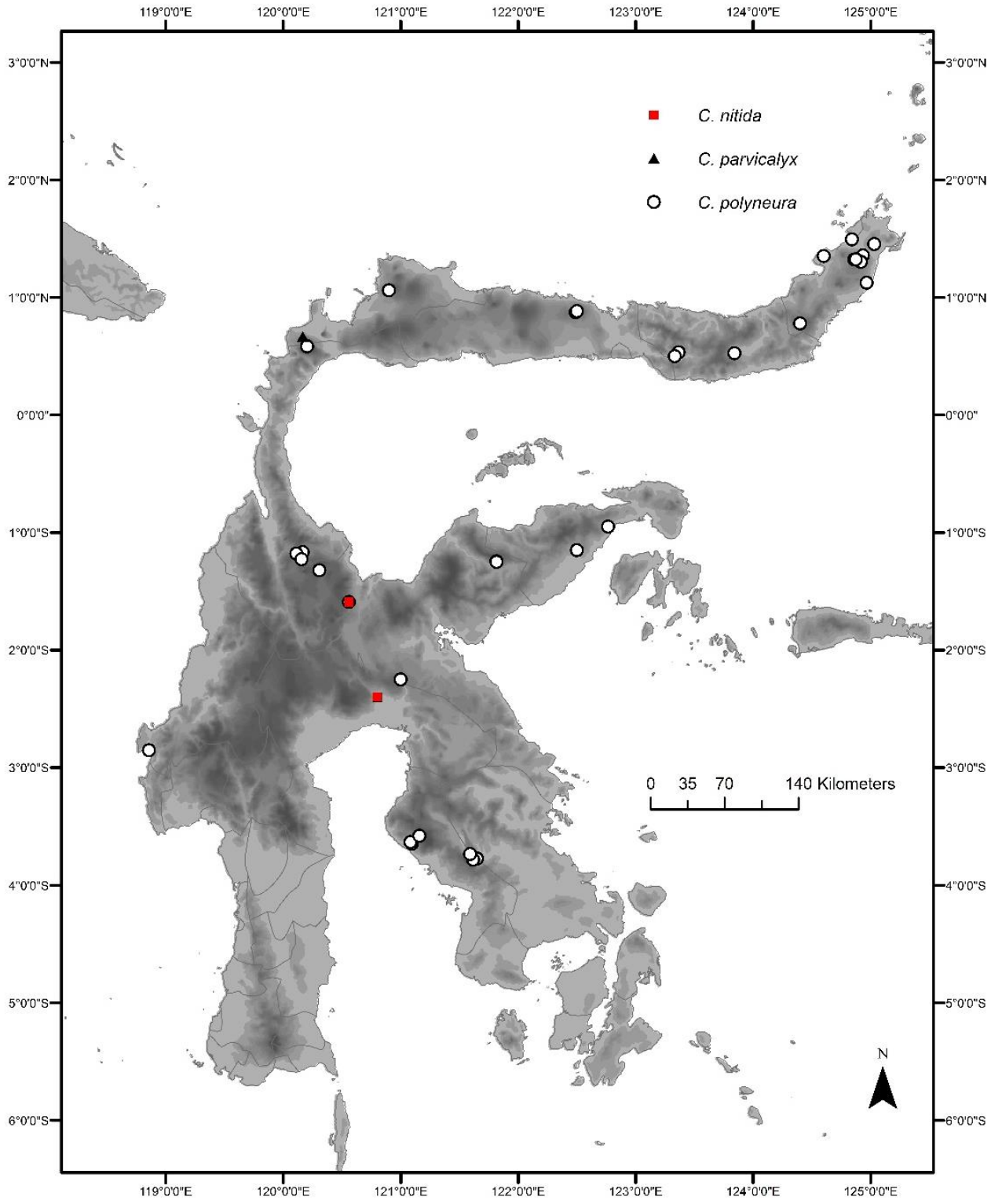


Fig. 2.42 Distribution of *Cyrtandra nitida* (red square), *C. parvicalyx* (black triangle) and *C. polyneura* (white circles).

Cyrtandra purpurea H.J.Atkins, Edinburgh J. Bot. 60(3): 313 (2004). – Type: Central Sulawesi, Upper Sopu River, 25 v 1979, *van Balgooy* 3503 (holotype L; isotypes A, BO, E). **Fig. 2.43**

Branching, ***epiphytic climber*** or ***shrub*** (height not recorded). ***Stems*** striate, subglabrous. ***Leaves*** opposite, subequal; petiole 10–20 mm long, glabrous; blades 17–22 × 4–5 cm, narrowly oblong, apex acuminate, base narrowly cuneate, slightly decurrent, margin entire; 11–14 pairs of lateral veins, not reaching margin, tertiary venation obscure, glabrous above, sparsely hairy on midrib and veins below. ***Inflorescences*** axillary, sessile, 1–2-flowered, from near apex to base of stem; bracts not seen (soon caducous?), pedicels up to 15 mm long, extending in fruit, glabrous. ***Calyx*** tubular, purple, coriaceous, 10-11 mm long, 5-lobed, slightly bilabiate, lobes triangular, 5 mm long, glabrous. ***Corolla*** purple to brown, 30 mm long, tubular, glabrous externally, mouth oblique, limb strongly bilabiate, lower median lobe linear and strongly recurved, c. 8 × 1.5 mm, upper and lateral lobes recurved, 2–3 mm long. ***Stamens*** with filaments 20 mm long, attached 10 mm from base of corolla; anthers not seen (damaged on all specimens); staminodes 3, lateral staminodes c. 1 mm long, central staminode minute, barely visible. ***Gynoecium*** 35 mm long; disc cupular, margin subentire to undulate, 1 mm long, glabrous; ovary glabrous; style glandular hairy for much of its length; stigma peltate, 2 mm across, exserted. ***Fruits*** subglobose, fleshy, 10–17 × 10–12 mm, green when unripe, glabrous, calyx not persistent, base of style persistent.

Distribution. Central Sulawesi (Fig. 2.46).

Habitat and ecology. Upland forest at an altitude of 940 to 1000m.

Etymology. This species is named for the unusual purple colour of its corolla (Atkins, 2004).

Proposed IUCN conservation category. The low number of collection localities means that it has not been possible to calculate the EOO for this species but it has an AOO of 8 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). In addition to the collections from the Sopu Valley in 1979 (all with the same co-ordinates), this species has only been collected on one other occasion, in 2000, despite this being one of the better collected areas of

Sulawesi. All of the collections are from upland forest between 940 and 1000m which is one of the more threatened forest types on the island (Cannon et al., 2007) although they were all made in or very close to the boundary of Lore Lindu National Park (UNEP-WCMC & IUCN, 2019). Given the low number of collections and the lack of clarity about protection and potential threat, this species is considered to be Vulnerable under the Category VUD2.

Additional specimens examined: **Central Sulawesi**. Sopu Valley, 1000 m, 3 v 1979, *van Balgooy* 3124 (A, BO, E, L); Sopu Valley, 1000 m, 6 v 1979, *de Vogel* 5231 (BO, K, L); Kec Palolo, Kamarora, Gunung Potong, 940m, 17 xi 2000, *Kessler* PK2892 (K, L).

Sulawesi Group 8 (Atkins et al., Chapter Three).

Notes: This species is very distinctive due to its epiphytic habit, subglobose fruit, purple flowers with characteristic elongated lower lobe and leathery oblong leaves with obscure tertiary venation. There is a collection from Gunung Potong where the label states that there are four seeds in the fruit which would not be correct for *Cyrtandra.* It has not been possible to dissect the fruit to confirm this but assume that this is an incorrect observation, possibly of an immature fruit, of the four intrusive arms of the placentae.

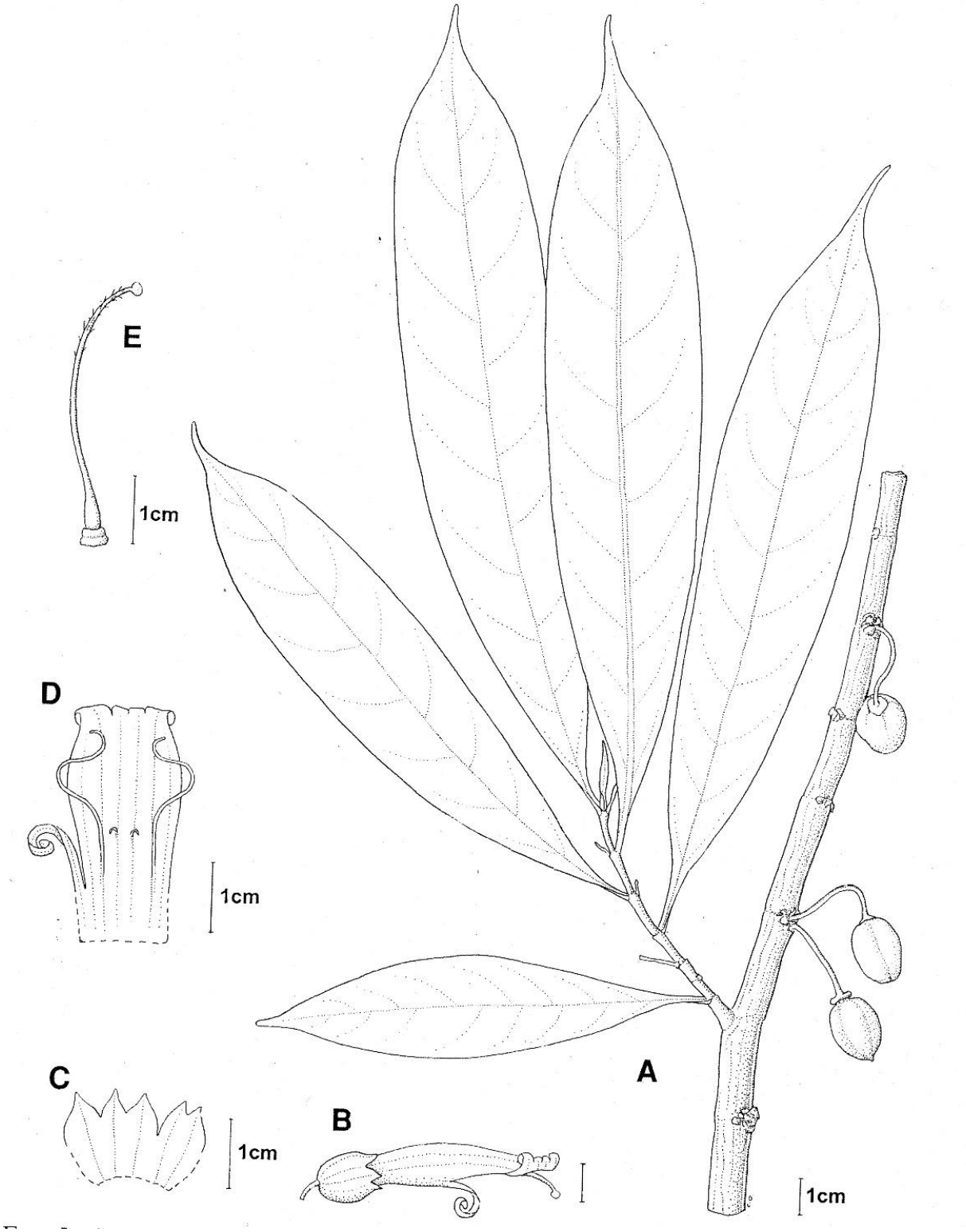


Fig. 2.43 Line illustration of *Cyrtandra purpurea* showing a. Habit b. Side view of corolla c. Opened calyx showing inner surface d. Opened corolla showing position of stamens and staminodes e. Gynoecium including disc. Drawn by Christina Oliver from *van Balgooy* 3503. Reproduced from Atkins (2004).

Cyrtandra purpureofucata R.Bone & H.J.Atkins, Edinburgh J. Bot. 70(3): 461 (2013) – Type: Sulawesi, Gunung Rantemario, 26 iv 2009, *Thomas & Ardi* 09-88 (holotype E, isotypes BO, L). **Fig. 2.44 & 2.45**

Herb or ***shrub*** 1 to 4 m in height. ***Stems*** woody, terete, warty, hairy, densely so when young. ***Leaves*** sub-equal to markedly anisophyllous or pseudo-alternate; petiole 6–10 mm long, hairy; blades of larger leaves 4.5–10 × 1.5–3 cm, elliptic to somewhat obovate, apex acuminate, base cuneate, margin serrate; 5–8 pairs of lateral veins, very prominent below on dried specimens, upper surface glabrous, lower surface with appressed hairs on primary and secondary veins, glabrescent between veins, juvenile leaves more densely hairy. Reduced leaves (where present) 1-2 cm x 0.5-1 cm, elliptic. ***Inflorescences*** axillary, sessile, 1–2-flowered; bracts 2–5 mm long, sometimes caducous, linear, hairy; pedicels 5–19 mm, densely hairy. ***Calyx*** green, coriaceous, 11–15 mm long, more or less evenly 5-lobed but with the division on the lower side slightly deeper; lobes 4–10 mm long, apex narrowly caudate to linear, hairy externally. ***Corolla*** deep pink externally, pale pink internally with dark purple lobes, 25–37 mm long; tube narrow in basal half becoming wider and pouched in apical half, narrowing again at mouth; lobes strongly recurved, the lower and lateral lobes being slightly larger than the upper two, c. 4 × 4 mm, densely hairy externally becoming sparsely glandular hairy on lobes. ***Stamens*** with filaments 9–11 mm long, glabrous, or with tuft of hairs at point of fusion with corolla tube, attached c. 20 mm from base of corolla; anthers facing one another and cohering at tips before dehiscence, 1–2 mm long; staminodes 3, lateral staminodes c. 3 mm long, central staminode slightly longer and thinner, c .4 mm long. ***Gynoecium*** 25–32 mm long; disc cupular, undulate with lobed, fringed margin, c. 2 mm long, glabrous; ovary and style densely eglandular hairy; stigma capitate to flattened. ***Fruits*** narrowly ovoid, asymmetric, c. 35 × 6 mm, hairy, base of style persistent, calyx persistent on young fruits.

Distribution. South Sulawesi: Rantemario (Fig. 2.46)

Habitat and ecology. In Tropalpine forest at an altitude of 2500–3000 m.

Etymology. The epithet 'purpureofucata,' meaning painted purple, refers to the strong colouring on the reflexed corolla lobes (Bone & Atkins, 2013).

*Proposed IUCN conservation category***.** This species has an EOO of 1 km^2 and an AOO of 12 km^2 based on a 2 x 2 km grid cell under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). *Cyrtandra purpureofucata,* has been collected on botanical expeditions to montane areas of South Sulawesi in

1929, 1937 and more recently in 2000 and 2009. All four specimens were collected in Tropalpine vegetation at 2500 to 3000 m. Tropalpine and Montane forests were ranked as the least endangered habitats of Sulawesi by Cannon *et al.* (2007), with a high proportion of Tropalpine forest classed as 'Great to Good' in quality. The lack of identifiable threats or evidence of decline precludes any of the IUCN threat categories so following Bone & Atkins (2013) this species is considered Least Concern (LC).

Additional specimens examined. **South Sulawesi**: Tinabang, West side of the Rante Mario, 3000 m, 17 vi 1937, *Eyma* 696 (A, BO, K, L, SING); B. Rante Mario [Buntu Rantemario], 2500 m, vi 1929, *Kjellberg* 4039 (BO, S); Rantemario, above Rantelemo, 2800 m, 6 iii 2000, *Mendum, Argent & Hendrian* 00252 (BO, E, K, L).

Sulawesi Group 14 (Atkins et al., Chapter Three).

Notes. This is a very distinctive species with its purple, pouched corolla with small, recurved lobes.

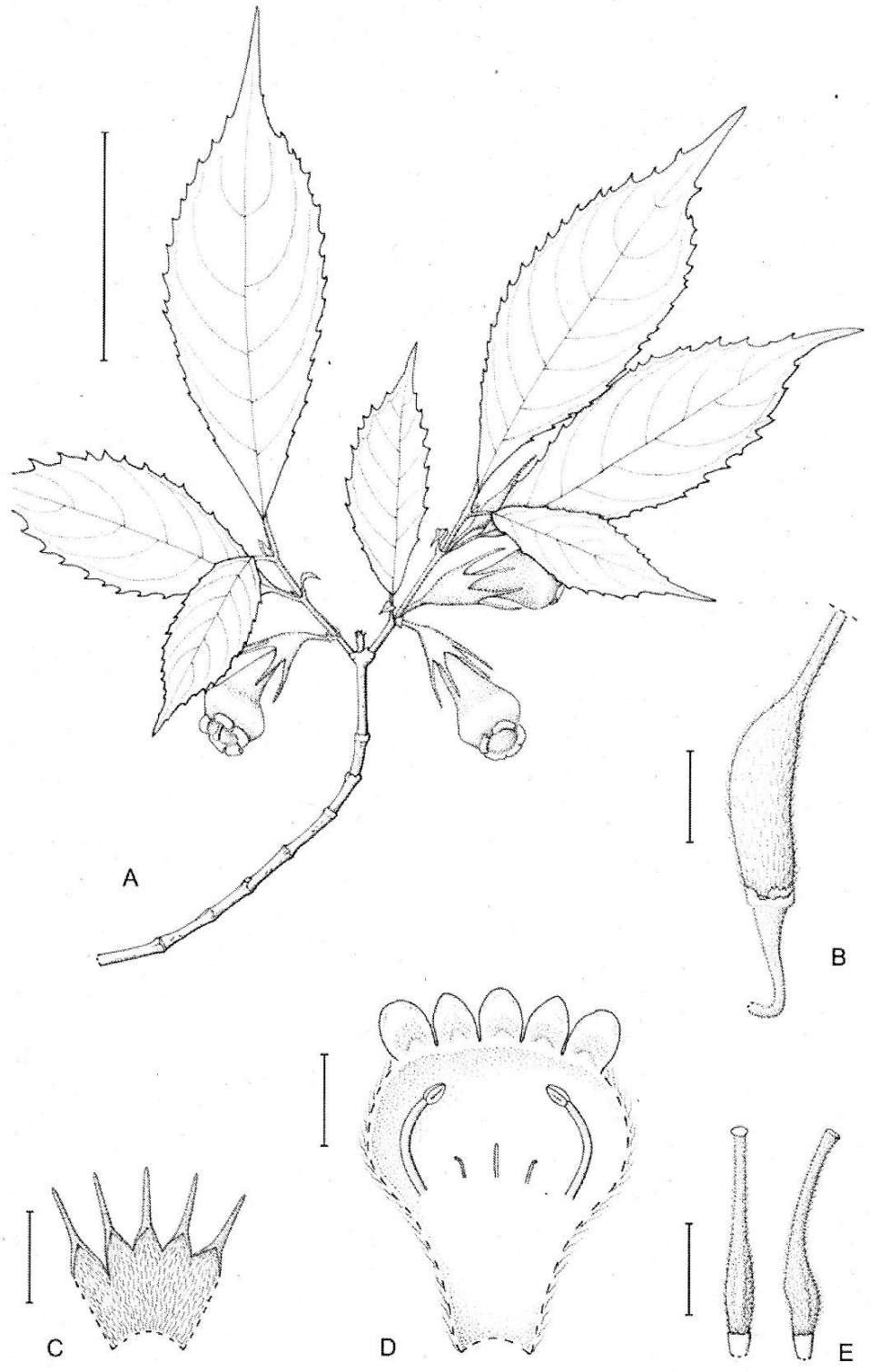


Fig. 2.44 Line illustration of *Cyrtandra purpureofucata* showing a. Habit b. Fruit c. Opened calyx showing inner surface d. Opened corolla showing position of stamens and staminodes e. Gynoecium and disc. Drawn by Claire Banks from *Thomas & Ardi* 09-88. Reproduced from Bone & Atkins (2013).

Fig. 2.45 Plate of *Cyrtandra purpureofucata* showing a. habit b. fruit c. front view of corolla d. view of corolla from above e. side view of corolla.f. leaves. Photos: Wisnu Ardi. Thomas & Ardi 09-88.

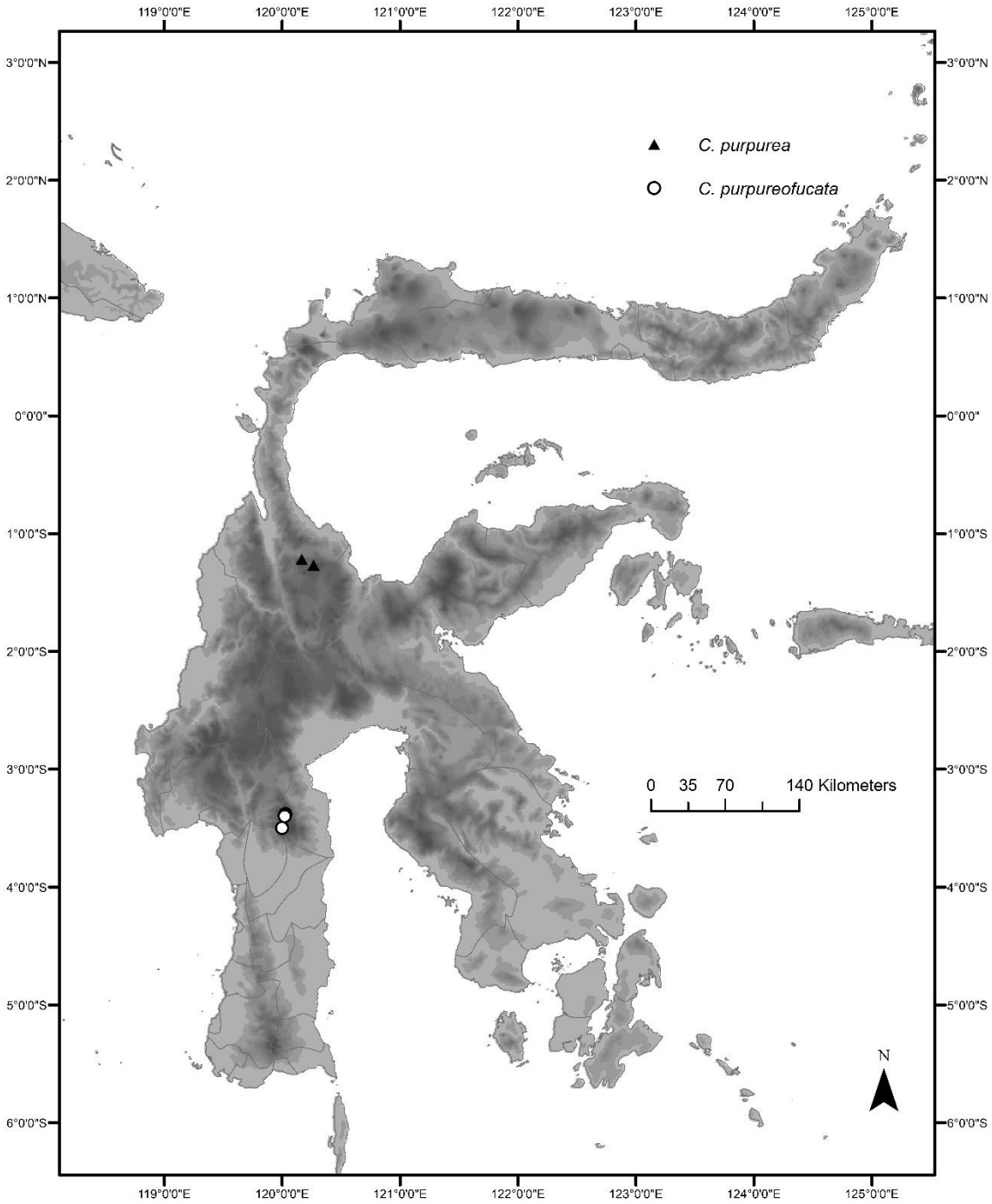


Fig. 2.46 Distribution of *Cyrtandra purpurea* (black triangles) and *C. purpureofucata* (white circles).

Cyrtandra rantemarioensis Karton. & R.Bone, Edinburgh J. Bot. 75(2): 26 (2018) – Type: Sulawesi, Gunung Rantemario, 5 iii 2000, *Mendum* et al. 00240 (holotype BO; isotypes E, L). **Fig. 2.47**

Branching subshrub to 2 m in height, often much shorter. ***Stems*** striate, greenish brown, glabrate, sparsely hairy on young growth. ***Leaves*** opposite, sometimes clustered at the ends of the stems, more or less equal; petioles 1.5–2 cm long, sparsely hairy; blades 8–20 x 1.8–5 cm, oblong to narrowly obovate, apex short acuminate, base attenuate to very narrowly winged at base, margin serrate; 5–6 pairs of lateral veins, tertiary venation loosely reticulate, mid to dark green, somewhat marbled and subglabrous to sparsely hairy above, much paler and flushed purple and subglabrous below, very sparsely hairy on midrib and veins. ***Inflorescences*** borne on trailing stems from the base of the plant, 40–50 cm or more long, subsessile, inflorescence stem striate, hairy when young, becoming glabrous with age, c. 1 mm in diameter with persistent bracteoles; bracts green to dull red, c. 25 x 10 mm, acuminate at apex, with serrate margins apically, hairy when young, particularly at the base and along veins, soon caducous, visible only at the tips of the inflorescence stems; bracteoles green to dull red, 10–15 x 2 mm, linear to linear–lanceolate, acuminate at apex, sparsely hairy externally, often persistent on inflorescence stem; pedicels reddish, 10–15 mm long, hairy, elongating and becoming more glabrous in fruit. ***Calyx*** reddish when in flower turning olive green when fruiting, c. 6 mm long, upper lobes divided briefly at apex, lower lobes free to base, lobes acuminate, sparsely hairy externally. ***Corolla*** red, slightly paler in the mouth, 15–20 mm long, arcuate with a narrow tube widening to mouth, sparsely hairy externally, internally with scattered eglandular hairs and a dense covering of glandular hairs in the mouth, lobes spreading, slightly projected forwards, two upper lobes orbicular, c. 7 x 7mm, lateral and lower lobes orbicular, 9–10 x 8 mm. ***Stamens*** with filaments c. 2mm, attached c. 12 mm above the base of the corolla, white, glabrous; anthers 1–2 mm long, cohering at apices, glabrous, white; staminodes 3, c. 0.5 mm long. ***Gynoecium*** c. 10 mm long; disc 2 mm long, unilateral with undulate to lobed margin, glabrous; ovary densely hairy; style glandular hairy towards apex; stigma bilobed, lobes vertical, c. 1 mm across. ***Fruits*** oblong, glabrous, smooth, greenish-brown (drying light brown), 15–30 x 4–8 mm; base of style and calyx persistent.

Distribution. South Sulawesi: Latimojong Range (Fig. 2.50).

Habitat and ecology. Montane forest at an altidue of 1500–2600 m.

Etymology. Named after the mountain from where the type specimen was collected (Kartonegoro et al., 2018).

Proposed IUCN conservation category. The EOO of this species is 195 km^2 and the AOO is 24 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). It has been collected on eight different botanical expeditions in the Latimojong Range (between 1969 and 2010) suggesting it is locally abundant and is found in montane forest *sensu* Cannon *et al*. (2007) which is one of the least threatened forest types in Sulawesi (70% of upland forests above 1500m elevation are intact). For this reason, and following Kartonegoro et al. (2018) it is recommended that this species be considered as Least Concern (LC).

Additional specimens examined. **South Sulawesi:** Latimojong Mts, Enrekang District, 28 i 2009*, Ardiyani, Poulsen & Firdaus 165* (E); Latimojong Mts, on path to Mt Rantemario peak, 6 vii 2002, *Brown, Craven & Juswara 4* (BO); Enrekang, 15 vi 1937*, Eyma 467* (BO, L); Rantemario, Buntu Kaciling, 11 vi 2010, *Kartonegoro & Santoso ARK475* (BO); Rantelemo, v 1929*, Kjellberg 4040* (BO); Latimojong Mts, Enrekang District, 30 x 1969*, Sands 307* (K); Mt Rantemario, 5 iii 2000, *Smith & Galloway* 229, grown at RBGE as accession 20000622K, vouchered as *Scott* 507 (E); Enrekang, Rantemario, 23 iv 2009*, Thomas & Ardi, 09-79* (BO, E); Gunung Rantemario, 24 iv 2009, *Thomas & Ardi* 09-81 (BO, E, L).

Sulawesi Group 4 (Atkins et al., Chapter Three).

Notes. This is one of four species in Sulawesi that have long, trailing inflorescence stems which originate at the base of the plant (others are: *C. hypogaea* Koord., *C. luteiflora* H.J. Atkins and *C. geocarpa* Koord.). This species can most easily be distinguished in this group by its red flowers and oblong fruits that although wrinkled when dry are not as distinctly tesselate as the fruits of *C. hypogaea*.

Fig. 2.47. Plate of *Cyrtandra rantemarioensis* showing a. habit b. trailing inflorescence c. front view of flower d. young fruits e. side view of flower. Photos: a- d: Axel Poulsen e: Steve Scott. Reproduced from Kartonegoro et al. (2018).

Cyrtandra roseiflora H.J.Atkins, Edinburgh J. Bot. 60(3): 318 (2004). Type: Sulawesi, Mt Sojol, 26 ii 2000, *Mendum* et al. 00173 (holotype BO; isotypes E, L). **Fig. 2.48**

Shrub to 1 m in height. ***Stems*** slender, striate, subglabrous. ***Leaves*** opposite, subequal or one in each pair markedly reduced; petiole 3–4 mm long, subglabrous; blades of developed leaves 6–11 × 1.5–3 cm, narrowly oblong to narrowly elliptic, apex acuminate, base cuneate and more or less symmetric at base, not decurrent, margin serrate; 5–7 pairs of lateral veins, occasionally looping and joining with vein above and with short veins running to the teeth, glabrous above and below. Reduced leaves 4 × 2 mm, cordate. ***Inflorescences*** axillary and at the base of stems in axils of fallen leaves, 1–2-flowered, sessile; pedicel 5–7 mm, sparsely hairy; bracts 2–4 mm long, linear, sparsely hairy, not connate. ***Calyx*** narrowly campanulate, pale green, 12–14 mm long, slightly bilabiate, lobes subulate, upper lobes c. 6 mm long,lower lobes c. 7 mm long, sparsely hairy. ***Corolla*** pale red outside, paler internally, in tube and throat, 30–35 mm long, narrowly funnel-shaped, gradually widening to mouth, slightly pouched on lower side, arcuate, held more or less erect, lobes rounded,not recurved, c 7 mm x 7mm, hairy externally, subglabrous internally. ***Stamens*** with filaments 3–5 mm long, attached 20–22 mm from base of corolla, glabrous; anthers 2 mm long, cohering at apices and face to face before dehiscence; staminodes two, less than 1 mm long. ***Gynoecium*** 11–22 mm long; disc cupular, with undulate, fringed margin, 2–2.5 mm long; ovary and style eglandular hairy; stigma bilobed, lobes 1 mm, pressed together. ***Fruits*** ovoid, 5 × 3 mm (immature?), sparsely hairy, calyx and base of style persistent.

Distribution: Central and South Sulawesi (Fig. 2.50).

Habitat and ecology. Montane forest at an altitude of 1500-1800 m.

Etymology. This species is named for its pink flowers (Atkins, 2004).

Proposed IUCN conservation category. This species is only known from two locations so it has not been possible to calculate an EOO but it has an AOO of 8 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). The Type collection is from Gunung Sojol

in Central Sulawesi which has protected status (UNEP-WCMC & IUCN, 2019) and the second is from Gunung Sesean which has no formal protection. They are both from montane forest at altitudes of 1500 and 1800m, which is less threatened than lowland areas with 70% of forest at this altitude in good (G2G) condition (Cannon et al., 2007). It is suggested that this species is considered Least Concern.

Additional specimens examined: **South Sulawesi**. Gunung Sesean, 7 xi 2018, *Ardi* WI345 (KRB).

Sulawesi Group 14 (Atkins et al., Chapter Three).

Notes. This species can be distinguished from others in Sulawesi by its glabrous, serrate leaves and pink flowers with white throat. The specimen *Rachmat* 1002a cited under the original description, is part of a mixed collection with most sheets containing a different species. To avoid later confusion, this specimen has not been included in the list of additional collections here.

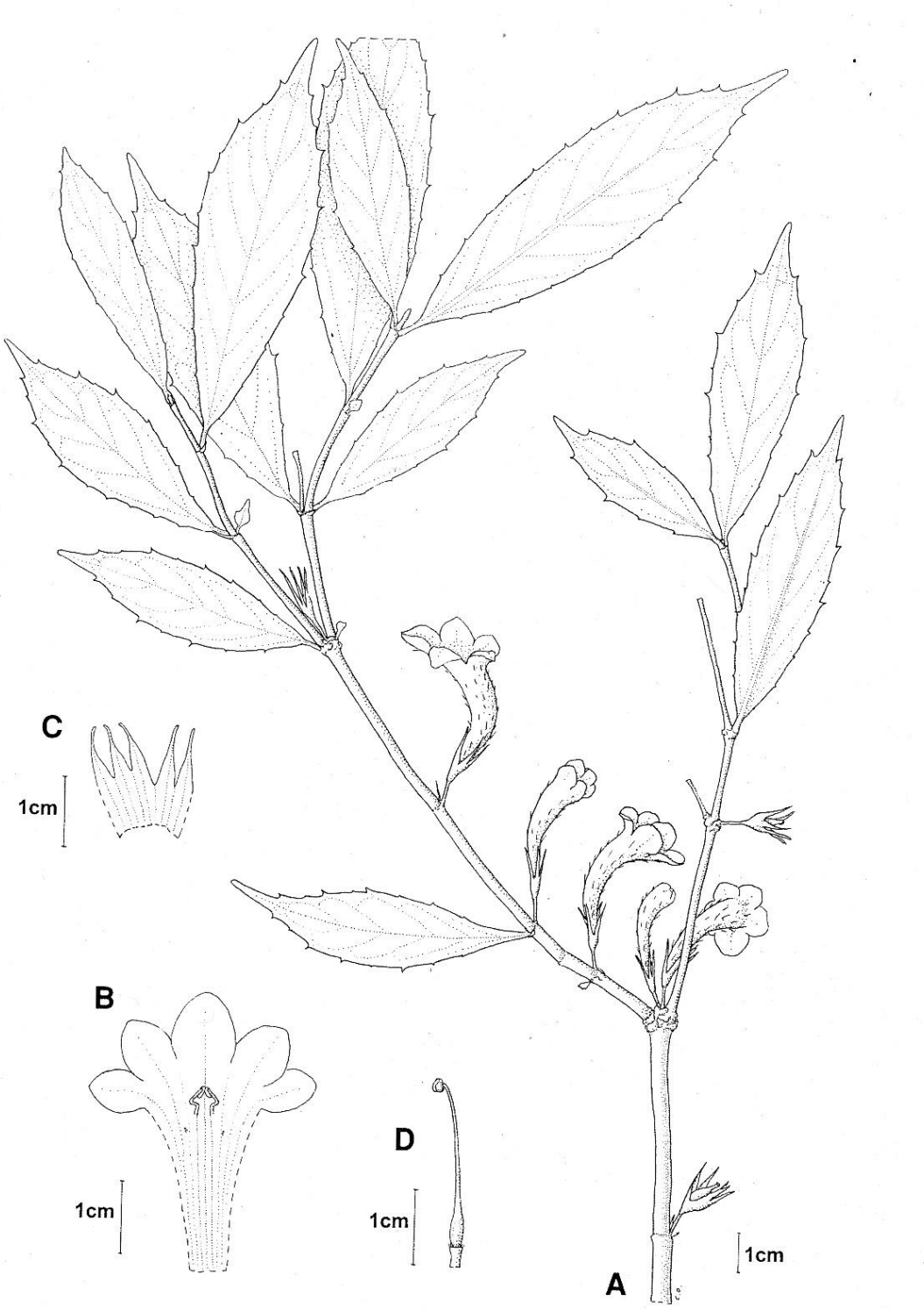


Fig. 2.48 Line illustration of *Cyrtandra roseiflora* showing a. Habit b. Opened corolla showing position of stamens and staminodes c. Opened calyx showing inner surface d. Gynoecium including disc. Drawn by Christina Oliver from *Mendum* et al. 00173. Reproduced from Atkins (2004).

Cyrtandra rubribracteata Karton. & H.J.Atkins, Edinburgh J. Bot. 75(2): 29 (2018) – Type: Sulawesi, Luwuk Regency, Mt Hek, 28 ii 2004, *Hendrian, Newman, Scott, Saleh. & Supriadi.* 968 (holotype BO; isotype E). **Fig. 2.49**

Shrub or treelet to 1.8 m in height. ***Stems*** cylindrical, striate, glabrous. ***Leaves*** opposite, subequal; petioles 1.5–2 cm long, glabrous; blades 14–25 x 2–3.5 cm, narrowly oblong to lanceolate, apex acuminate, base attenuate, margin serrate, occasionally biserrate; 5–7 pairs of lateral veins curving sharply upwards and faint tertiary venation, dark green and glabrous above, whitish-green and glabrous below. ***Inflorescences*** axillary, sessile, c. 6-flowered; bracts ovate, paired, dark, dull red, 3 x 2 cm, tough, leathery, joined very briefly at the base and forming an involucre with serrate margins, glabrous externally, enclosing the flowers and fruit; bracteoles c. 4 x 1 cm, some much smaller, narrow-lanceolate with serrate margins, leathery, glabrous; pedicels 4–6 mm long, hairy. ***Calyx*** tubular, pink, 30–36 mm long , lobes 9–17 mm long, acuminate, ridged along the length of the tips, hairy externally. ***Corolla*** white, 42–45 mm long, held upright in involucre, narrow in basal third, widening to mouth in upper two thirds, upper lobes rounded, 5–6 x 4–5 mm, lower and lateral lobes rounded 8–9 x 7–8 mm, distinctive ridges running along base of the tube, densely hairy externally. ***Stamens*** with filaments c. 10 mm long, attached c. 20 mm above the base of the corolla, straight at the base, curved over slightly at the top, glabrous with a few glandular hairs at the apex; anthers c. 1 mm long, glabrous, drying much darker than the filaments, with a distinctive pointed tip appearing like a hook or beak, not coherent; staminodes 3, c. 5 mm long. ***Gynoecium*** c. 30 mm long; disc cupular with undulate margin, c. 2 mm long, glabrous; ovary glabrous at the base becoming densely hairy after c. 4mm with the margin of indumentum somewhat lobed; style densely hairy; stigma bilobed, lobes vertical or spreading, c. 3 x 2 mm, with short glandular hairs. ***Fruits*** ovoid (immature), c. 15 x 11 mm, glabrous at the base, more densely hairy at apex; style and calyx not persistent.

Distribution: Central Sulawesi: Luwuk (Fig. 2.50).

Habitat and ecology. Upland forest at an altitude of c. 980 m.

Etymology. This species is named for its distinctive red bracts (Kartonegoro et al., 2018).

Proposed IUCN conservation category. A lack of specimens of *Cyrtandra rubribracteata* precludes an estimation of EOO but the species has an AOO of 8 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). It has only been possible to accurately georeference one of the collections, the Type specimen from Mt Hek in Central Sulawesi. This area does not receive any formal protection (UNEP-WCMC & IUCN, 2019) and the collection is from 980 m which is one of the more threatened habitat types in Sulawesi (Cannon et al., 2007). Following Kartonegoro et al. (2018), the category Vulnerable (VU) is given for this species using the criteria VUD2 as it is a population with a very restricted area of occupancy or number of locations.

Additional specimens examined. **Central Sulawesi:** Luwuk Regency, between Camp I and Camp II, 28 ix 1938*, Eyma 3909* (BO, K, L).

Sulawesi Group 2 (Atkins et al., Chapter Three).

Notes. This species can be distinguished from other Sulawesi *Cyrtandra* by its narrowly oblong leaves with serrate margins, large, dull red inflorescence bracts and unusual, somewhat beaked, anthers. No other species from Sulawesi recorded so far has these distinctive anther appendages. There are, however, a number of species from Borneo recorded with a 'conspicuous apiculus' on the anthers such as *C. prostrata* Kraenzl. and *C. paxiana* Lauterb.

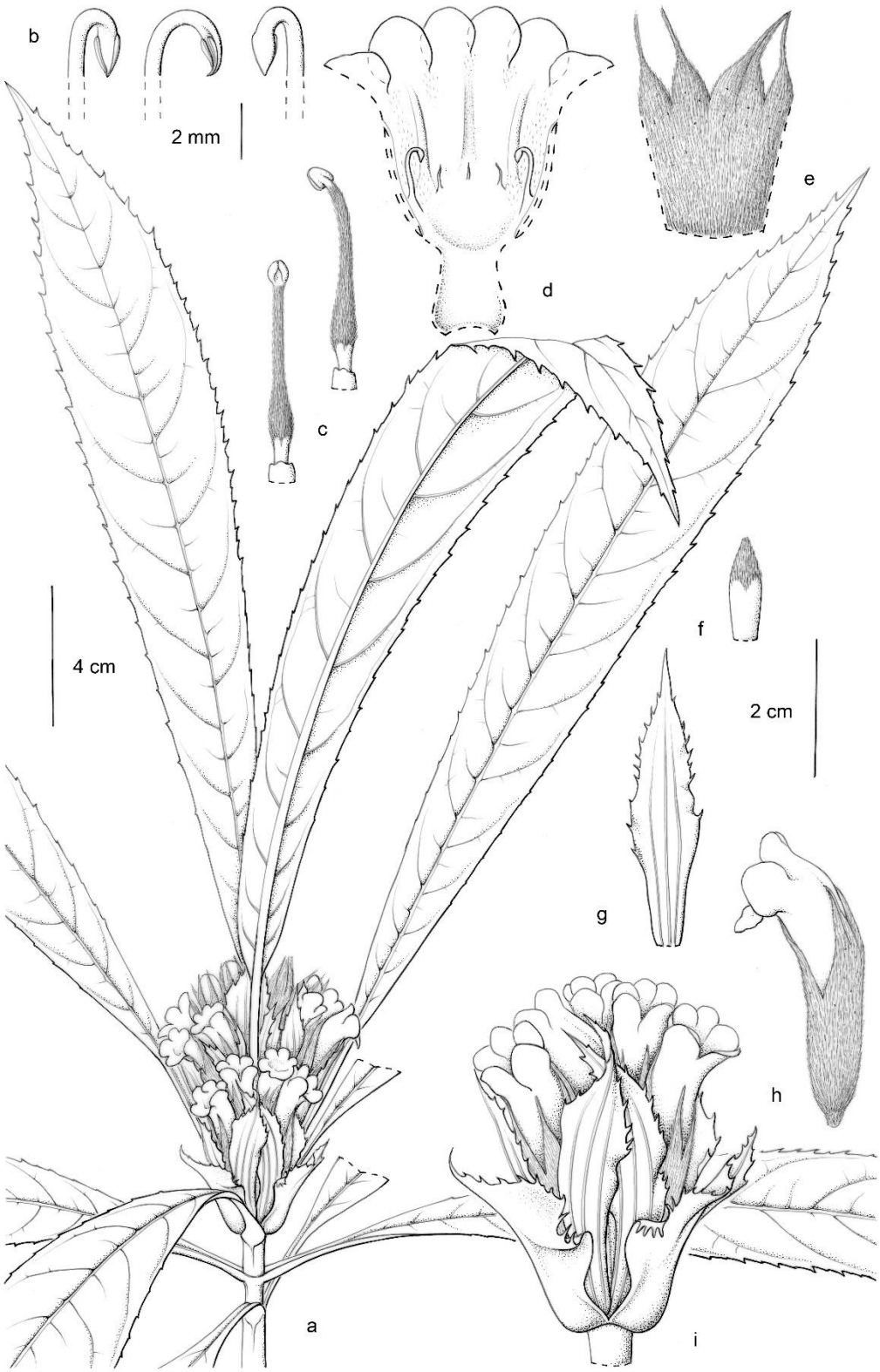


Fig. 2.49 Line illustration of *Cyrtandra rubribracteata* Atkins showing a. Habit b. Anthers c. Gynoecium including disc d. Opened corolla showing position of stamens and staminodes e. Opened calyx f. Fruit g. Bracteole h. Side view of corolla i. Inflorescence. Drawn by Claire Banks from *Hendrian* et al. 968. Reproduced from Kartonegoro et al. (2018).

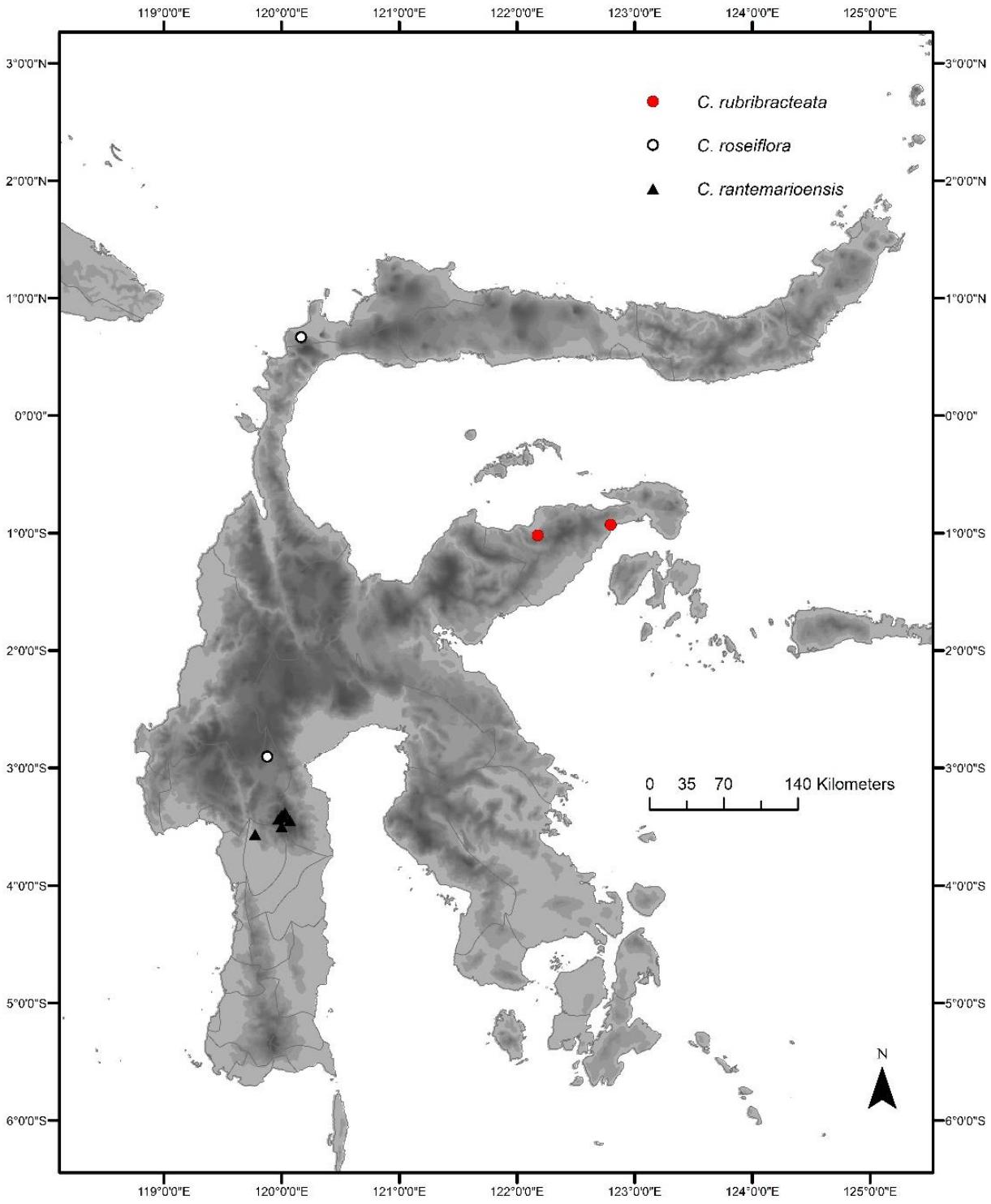


Fig. 2.50 Distribution of *Cyrtandra rantemarioensis* (black triangles), *C. roseiflora* (white circles) and *C. rubribracteata* (red circles).

Cyrtandra sandei de Vriese, Pl. Ind. Bat. Orient. 14 (1856) – Type: Celebes [Sulawesi], Lontar, *Reinwardt* 218 (holotype L). **Fig. 2.51**

Shrub to 2m in height. ***Leaves*** opposite, subequal; petioles 10 mm long, sparsely hairy; blades 16–19 cm x 5–9 cm; narrow obovate, apex acuminate, base decurrent, margin serrate, 17–20 pairs of lateral veins, glabrous above, sparsely hairy below, more densely so on midrib and veins. ***Inflorescences*** axillary, often below current leaves; subsessile to shortly pedunculate; bracts narrow ovate, acuminate at apex, up to 12 mm x 3 mm, hairy. ***Calyx*** 6 mm long, lobes triangular, acuminate at apex, 2 mm long, hairy externally. ***Corolla*** pale green-yellow with reddish-brown markings in the throat, c. 18 mm long , narrow in basal third, widening to mouth in upper two thirds, upper lobes rounded, 2 mm x 3 mm, lower and lateral lobes rounded 3 mm x 4 mm, densely hairy externally. ***Stamens*** with filaments 6 mm long, glabrous with a few glandular hairs at the apex; anthers 1.5 mm long, face to face and connected at tips before dehiscence; staminodes 3, two lateral ones 1.5 mm long, central 0.5 mm long. ***Gynoecium*** c. 10 mm long; disc unilateral, 2 mm long, glabrous; ovary and style densely eglandular hairy, stigma bilobed, c. 1 mm across. ***Fruits*** oblong, c. 20 mm x 5 mm, hairy, calyx and base of style persistent.

Distribution: [Lontar] in Sulawesi (this locality could be Lota in North Sulawesi as all of Reinwardt's collection localities are in the north of the island and Lota is listed as one of these (van Steenis, 1950); Java and Sumatra.

*Habitat and ecology.*There is no information on the collection from Sulawesi but the collections from Java and Sumatra have been collected over a wide altitudinal range from 100-1400 m.

Etymology. This species is named after C.M. van der Sande Lacoste, a medical doctor and good friend of de Vriese who studied cryptogamic plants (de Vriese, 1856).

Proposed IUCN conservation category. This species is recorded from Sulawesi, Java (Bakhuizen van den Brink, 1950) and Sumatra (fide Bakhuizen K, L) and, as such, has one of the widest distributions of *Cyrtandra* species in the region. The locality of the single collection of *C. sandei* from Sulawesi,

which is the type, is not known so a category of Data Deficient is recommended for this species in Sulawesi but suggest it is considered of Least Concern across its full distribution.

Additional specimens examined. This species is only known in Sulawesi from the type specimen.

Sulawesi Group: 3 (Atkins et al., Chapter 3).

Notes. Cyrtandra sandei is most similar to *C. jellesmani* in having subequal, decurrent leaves, non-tesselate stems, narrow inflorescence bracts and densely eglandular hairy ovaries. It can be distinguished from this species, most easily, by its much smaller flowers (18 mm long vs 45 mm long) and unilateral as opposed to cupular nectary disc.

The description of *C. sandei* is brief and has been compiled from the single Sulawesi collection (the type specimen), de Vriese's original description, and supplemented with information from literature (Clarke, 1883; Bakhuisen van den Brink, 1950). The type from Sulawesi is a good match for the material in Sumatra and Java but a detailed review of all of the collections across the distribution of *C. sandei* is needed to confirm that the collections in Java, Sumatra and Sulawesi are all the same species and to capture the full intraspecific variation.

Fig. 2.51 Plate of *Cyrtandra sandei* showing a. stem and inflorescence b. close up of flower. Photos: Hannah Atkins. *Atkins* 5 (collected in Java).

Cyrtandra serratifolia H.J.Atkins, Edinburgh J. Bot. 60(3): 313 (2004). - Type: Sulawesi, Bolaang Mongondow, 16 iv 1985, *de Vogel & Vermeulen* 7202 (holotype BO; isotypes E, K, L). **Fig. 2.52**

Erect or creeping ***shrub*** to 30 cm in height. ***Stems*** longitudinally striate, hairy, more densely so when young. ***Leaves*** opposite, sometimes in threes; all well developed but somewhat unequal in size; petiole 1–4 mm long, hairy to densely hairy; blades 0.5–2 × 0.4–1.2 cm, elliptic to broadly elliptic, sometimes obovate, apex rounded to short acuminate, base broadly cuneate, margin serrate; 3–4 pairs of lateral veins, occasionally with short veins running to adjacent teeth, sparsely hairy, more densely so on midrib and margins above and midrib and veins below. ***Inflorescences*** axillary, subsessile, 1–2-flowered; bracts 3–5 × 1 mm, linear hairy; pedicels 4–5 mm, hairy. ***Calyx*** green, 7–9 mm long, with 5 equal subulate lobes, 5–6 mm long, hairy externally, most densely so at median line of lobes and at their tips. ***Corolla*** pink or red, 20–26 mm long, funnel-shaped, slightly arcuate, lobes rounded, upper lobes 5–6 × 7–8 mm, lower lobes 6–7 × 5–6 mm, hairy externally. ***Stamens*** with filaments 2 mm long, attached 12–14 mm from base of corolla, filaments with some sessile glands; anthers 1.5 mm long, cohering at apices before dehiscence; staminodes 3, all less than 1 mm long. ***Gynoecium*** 9–13 mm long; disc cupular, undulate, 1 mm long, glabrous; ovary subglabrous at base becoming glandular hairy towards style; style glandular hairy; stigma bilobed, lobes 3 mm across. ***Fruits*** ovoid, 10 × 5 mm (possibly immature), subglabrous but with glandular hairs at base of persistent style; calyx persistent.

Distribution. North Sulawesi and Gorontalo (Fig. 2.56).

Habitat and ecology. Upland and montane forest at an altitude of 1300-1800 m.

Etymology. This species is named for its distinctive serrate leaves (Atkins, 2004).

Proposed IUCN conservation category. The EOO of this species is 1,811 km^2 and the AOO is 20 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). The collections are from relatively high altitude forest which is less threatened in Sulawesi (Cannon et al., 2007) than the lowland areas and from within the protected areas of Gunung Ambang and Bogani Nani Wartabone National Park (UNEP-WCMC & IUCN, 2019). Given the distribution of this species, entirely within protected areas, a category of Least Concern is given for this species.

Additional specimens examined: **North Sulawesi**. Bolaang Mongondow, Gunung Ambang Nature Reserve, 2 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK44 (BO, E); East Bolaang Mongondow, Gunung Ambang, 3 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK54 (BO, E); Bolaang Mongondow, viii 1917, *Kaudern* 184 (BO); Dumoga Bone National Park, Bolaang Mongondow, 26 ix 1991 *Milliken* 1064 (E, L);
Gorontalo. Gunung Gambuta, 12 iv 2002 *Atkins* et al. 93 (BO, E); ibid., 12 iv 2002, *Scott* 02-82, grown on at RBGE as accession 20021210A, vouchered as *Cubey & Scott* 255 (E).

Sulawesi Group: 13 (Atkins et al., Chapter 3).

Notes: This species differs from any other yet seen from Sulawesi in its tiny serrate leaves and low scrambling habit. It does, however, share this habit and leaf shape with *C. tarsodes* B.L.Burtt from very high altitude areas in New Guinea and *C. auriculata* C.B.Clarke and *C. zamboengensis* Merr. from the Philippines. There seems to be some variation in corolla colour with the recent collections from Gunung Ambang having much brighter red corollas than those from Gunung Gambuta which are a paler, slightly metallic pink (see differences in Fig. 2.53). These differences were observed both in the wild populations and in cultivation.

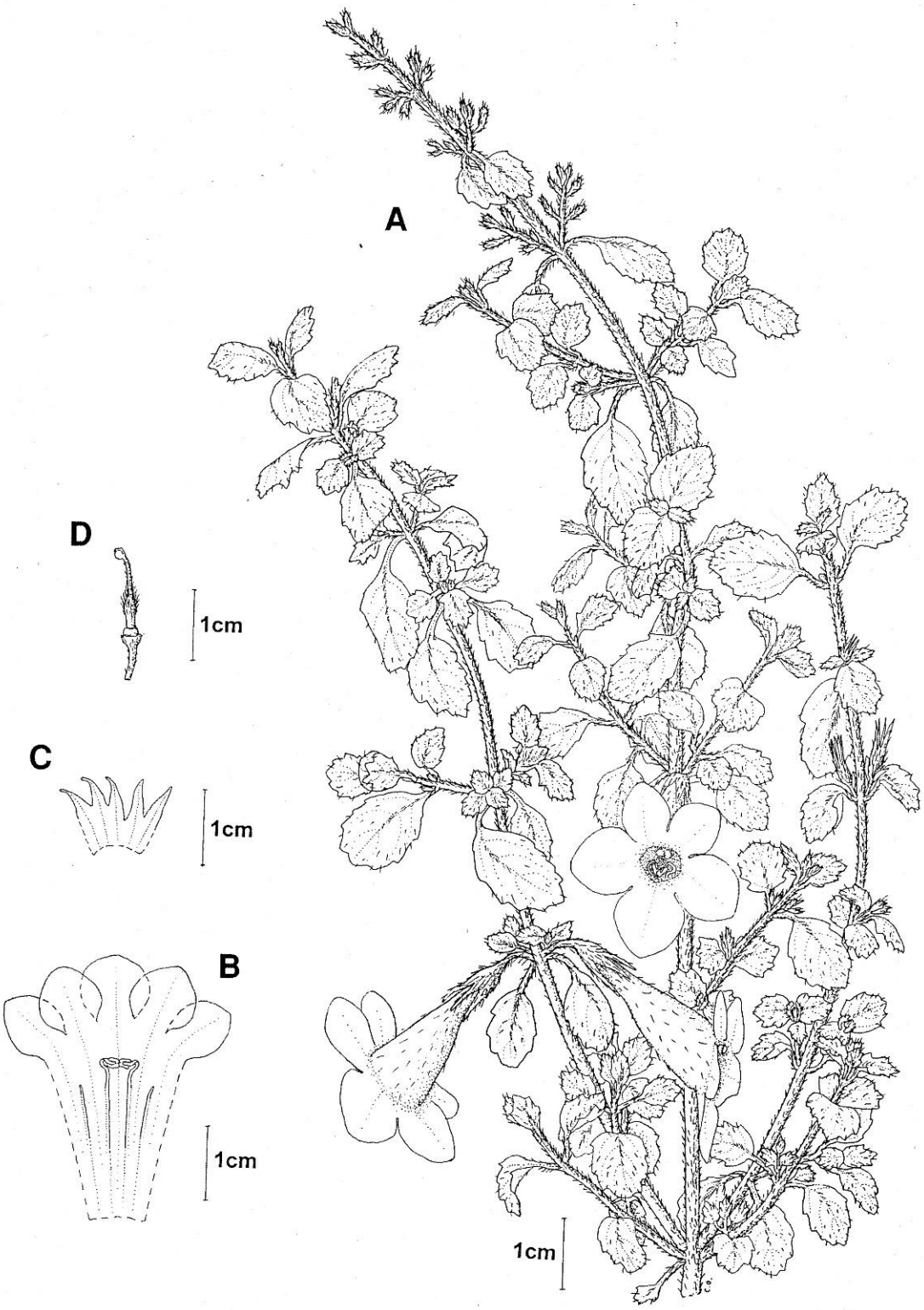


Fig. 2.52 Line illustration of *Cyrtandra serratifolia* showing a. Habit b. Opened corolla showing position of stamens and staminodes c. Opened calyx showing inner surface d. Gynoecium including disc. Drawn by Christina Oliver from *Atkins* et al. 93. Reproduced from Atkins (2004).

Fig. 2.53 Plate of *C. serratifolia* showing variation in flower colour between collections from different locations a. side view of corolla (BAKK54) b. habit (BAKK54) c. side view of corolla (Scott 02-82 grown on at RBGE as accession 20021210A) d. front view of corolla (Scott 02-82 grown on at RBGE as accession 20021210A). Photos: a&b: Sadie Barber. c&d. Hannah Atkins.

Cyrtandra sopuensis H.J.Atkins & Karton. **sp. nov.** ined**.**

Similar to *C. widjajae* in having markedly anisophyllous leaves, white, hairy flowers and and hairy fruits but distinguished by its smaller flowers (corollas 11–13 mm long in *C. sopuensis* vs corollas 15–20 mm long in *C. widjajae*), longer, and more numerous, inflorescence bracts (bracts 6–10 mm long in *C. sopuensis* vs bracts 2–3 mm long in *C. widjajae*) and scale-like, reduced leaves (as opposed to cordate, reduced leaves in *C. widjajae*). – Type: Sulawesi, Sopu Valley, 1 v 1979, *de Joncheere* 1134 (holotype L; isotype E). **Fig. 2.54**

Shrub or **small tree**, 1.5–2(–3) m in height. ***Stems*** striate, sparsely hairy. ***Leaves*** opposite with one leaf of a pair markedly reduced and scale-like or apparently alternate; petiole 5–10 mm long, sparsely hairy to hairy; blades (3–)11–13 cm × (1–)3–3.5 cm, narrow-elliptic or oblanceolate, apex long acuminate, base acute, margin subentire to crenate towards apex; 7–12 pairs of lateral veins, secondary veins curving upwards and running out to margin, reticulate tertiary venation, upper and lower surface of mature leaves subglabrous, sparsely hairy on midrib and veins. *Reduced leaf* usually scale-like, up to 10 mm long but also occasionally with a developed blade and petiole, very narrow elliptic, up to 10 mm x 3 mm. ***Inflorescences*** axillary**,** subsessile, up to 7–8-flowered, occasionally fewer; bracts 6–10 mm × 1–2 mm, linear, densely hairy; pedicels 2–3 mm long, densely hairy. ***Calyx*** campanulate, 5–7 mm long, densely hairy, evenly 5-lobed or with two lobes adpressed appearing 4-lobed, lobes subulate, 3–4 mm long. ***Corolla*** white, 11–13 mm long, tube narrower in basal two thirds, gradually widening to mouth in apical third, lobes rounded, slightly oblong, spreading, not strongly recurved, c. 2–3 mm × 1–2 mm, densely hairy externally, with a scattering of glandular hairs internally on inside of lobes and the base of the corolla tube. ***Stamens*** with filaments 3–4 mm long, attached 6–7 mm from base of corolla, glabrous; anthers 1 mm long, glabrous with a few glandular hairs at apex, connected at tips before dehiscence; staminodes 3, laterals 1 mm long, central less than 0.5 mm long. ***Gynoecium*** 9–11 mm long; disc cupular with lobed margin, 1-1.5 mm long, glabrous externally but with a fringe of hairs along the margin; ovary and style densely eglandular hairy; stigma slightly bilobed, 1 mm across. ***Fruit*** cylindrical to narrow ovoid, hairy, 10 mm × 3–4 mm, calyx not persistent, base of style persistent.

Distribution: Central Sulawesi (Fig. 2.54).

Habitat and ecology. Upland forest at an altitude of 1000 to 1300 m, sometimes in disturbed vegetation.

Etymology. This species is named after the Sopu Valley, the area of Central Sulawesi where it was collected.

Proposed IUCN conservation category. Although there are six collections of this species, all of the collections were made on the same expedition in April and May of 1979 to the Sopu Valley area of Central Sulawesi and share the same general co-ordinates. It has, therefore only been possible to calculate an AOO which is 4 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). The collections are from mid-altitude upland forest which is somewhat less threatened than lowland areas (Cannon et al., 2007) and close to the edge of, and possibly just within, the Lore Lindu National Park therefore afforded some protection (UNEP-WCMC & IUCN, 2019). This species is considered to be Least Concern.

Additional specimens examined: **Central Sulawesi**. Sopu Valley, c 80 km SSE of Palu, 27 iv 1979, *van Balgooy* 3037 (A, L); Sopu Valley, c.80 km SSE of Palu, 9 iv 1979, *de Vogel* 5097 (L, NSW); Sopu Valley, c 80 km S of Palu, 29 iv 1979, *Hennipman* 5111 (A, E, L, NSW); Sopu valley, trail to Puncak Dingin, 14 v 1979, *de Joncheere* 1281 (L); Sopu valley, 29 v 1979, *Hennipman* 5684 (A, L).

Sulawesi Group: 14 (Atkins et al., Chapter 3).

Notes. This species is most similar to the widespread *C. widjajae* and the narrow endemic *C. parvicalyx.* It can be distinguished most easily from *C. widjajae* by its scale-like as opposed to cordate reduced leaves and from *C. parvicalyx* by its persistent inflorescence bracts and larger leaves (11—13 cm long vs 6—9 cm) with more lateral veins (7-12 pairs vs 5 pairs).

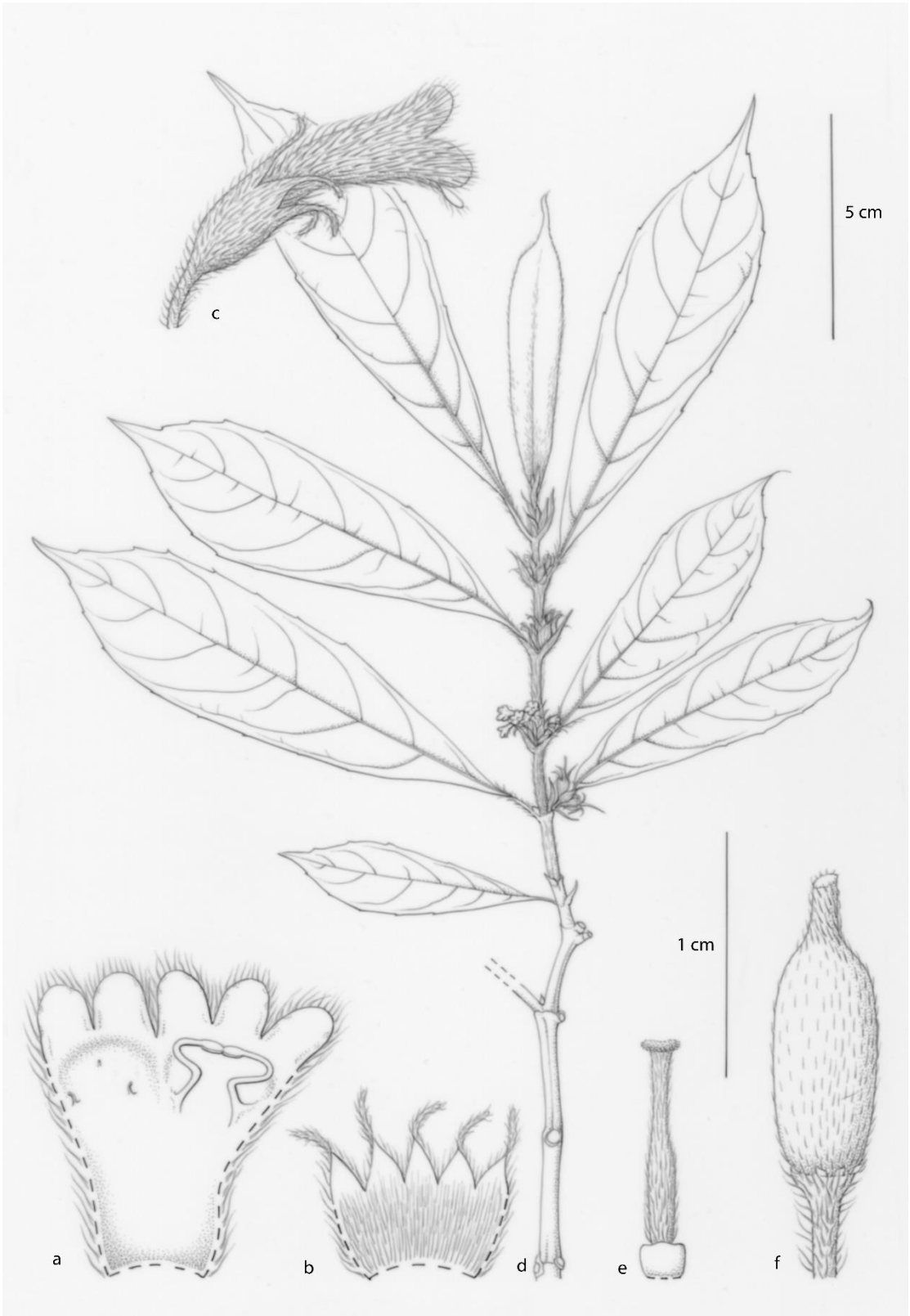


Fig. 2.54

Line illustration of *Cyrtandra sopuensis* showing a Opened corolla showing position of stamens and staminodes b. Opened calyx showing inner surface c. Side view of flower d. Habit e. Gynoecium and disc f. Fruit. Drawn by Claire Banks from *de Joncheere* 1134.

Cyrtandra spectabilis R.Bone & H.J.Atkins, Edinburgh J. Bot. 70(3): 463 (2013) − Type: Sulawesi, Subdivision Enrekang District, Latimojong Mountains, c. 1.5 km to the north of Bunte Tjejeng, 1 xi 1969, *Sands* 331 (holotype E; isotypes BO, K). **Fig. 2.55**

Erect, spreading ***shrub*** to 2.5 m in height. ***Stems*** terete, glabrescent or sparsely hairy. ***Leaves*** anisophyllous or appearing alternate; petiole 4–10 mm long, hairy; blades of larger leaves 8−11 × 2−3.2 cm, narrowly elliptic to narrowly obovate, apex acute, base cuneate, margin serrate, serrations irregularly and distantly spaced (c. 5–24 mm apart), with small tufts of hair at apex; 5–7 pairs of secondary veins, upper surface glabrous, lower surface hairy on midrib and veins, juvenile leaves more densely hairy. Reduced leaves (where present) elliptic, c. 10 mm x 4 mm. ***Inflorescences*** axillary, 1–2-flowered, or cauliflorus fascicles of up to 7 pendulous flowers; peduncle short, 2–4 mm, hairy; bracts c. 2–3 mm, linear to oblanceolate, hairy, leafy (with mid-rib); pedicel 30–40 mm, slender, glabrescent to sparsely hairy. ***Calyx*** maroon, 20–25 mm long, split on ventral side c. ¼ to ½ the length of the calyx, upper lobes c. 4–7 mm long (in immature flowers the calyx is not so deeply divided on the lower side and the calyx is more obscurely bilabiate), hairy externally. ***Corolla*** very pale lemon yellow to cream, 30–40 mm long, funnelform, tube narrow at base, gradually widening to mouth, lobes c. 7 mm × 6 mm, glabrous internally, eglandular hairy externally. ***Stamens*** with filaments 11 mm long, cream, glabrous, attached c. 24 mm from base of corolla; anthers 1.5 mm long, cohering at apices before anthesis; staminodes 3, lateral staminodes c. 1mm long, central less than 1 mm long. ***Gynoecium*** c. 30 mm long; disc cupular, undulate with lobed margin, c. 1.2 mm long, glabrous; ovary densely eglandular hairy; style white, sparsely glandular-hairy; stigma peltate, c. 0.8 mm across. ***Fruits*** not seen.

Distribution South Sulawesi: Latimojong Mountains (Fig. 2.56).

Habitat and ecology. Montane forest at an altitude of 1900 m.

Etymology. This striking species with large, yellow flowers and a purple calyx was given the epithet, *spectabilis,* meaning attractive (Bone & Atkins, 2013).

Proposed IUCN conservation category. *Cyrtandra spectabilis* is known only from the type material. The AOO of this species is 4 km^2 based on a 2 x 2 km grid cell size under the B criteria (Bachman et al., 2011) (map in Appendix 2.1). It was collected in 1969 from relatively high altitude and although Cannon *et al.* (2007) rank the threats to Montane forests in Sulawesi as low, 'moderate to strong

anthropogenic disturbance' has been reported in primary forest in the Latimojong Mountains between 1300 m and 2200 m asl (Thomas *et al.*, 2011) and there is no formal protection in this area (UNEP-WCMC & IUCN, 2019). Thus this species is considered as Vulnerable under the VUD2 category to reflect the perceived threat and its restricted distribution.

Additional specimens examined. This species is only known from the type specimen.

Sulawesi Group: 14 (Atkins et al., Chapter 3).

Notes. This is a very distinctive species with its pendulous yellow flowers and maroon membranaceous calyx. It is not like any other species in Sulawesi.

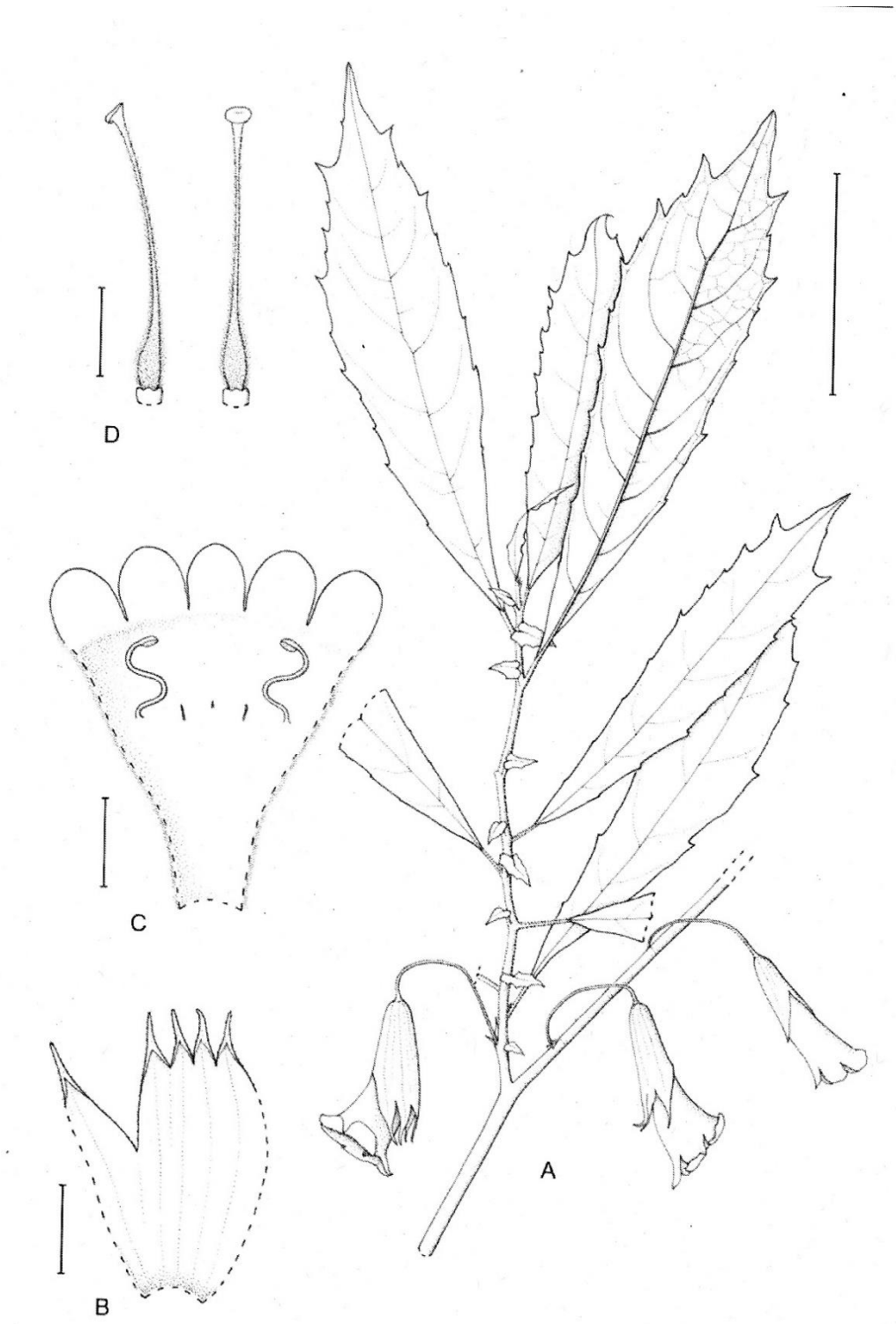


Fig. 2.55 Line illustration of *Cyrtandra spectabilis* showing a. Habit b. Opened calyx showing inner surface c. Opened corolla showing position of stamens and staminodes d. Gynoecium and disc. Drawn by Claire Banks from *Sands* 331. Reproduced from Bone & Atkins (2013).

Cyrtandra spicata de Vriese, Pl. Ind. Bat. Orient. 13 (1856). – *Rhynchocarpus spicatus* Reinw. ex de Vriese, Pl. Ind. Bat. Orient. 13 (1856) nom. nud. – Type: Celebes [Sulawesi], in sylvis montis Klabat, xi. 1821, *Reinwardt* 1571 (holotype L).

Shrub or ***small tree*** to 5m in height. ***Leaves*** opposite or in threes, crowded at ends of branches; those of a group or pair well developed but somewhat unequal in size; petiole up to 5 mm long, hairy; blades 15–25 cm × 4.5–8 cm, oblanceolate, apex acute, base decurrent and white, margin serrate-dentate; 7–9 pairs of lateral veins, curving upwards and running out to margin with some lateral veins running out to adjacent teeth, upper surface of leaves subglabrous, sparsely hairy below, more densely so on midrib and veins. ***Inflorescences*** spicate, pendulous from branches, inflorescence axis up to 25 cm long, many-flowered, flowers clustered terminally, axis appearing scaly from the remains of old bracts; bracts up to 25 mm long, broad, possibly ovate, sparsely hairy. ***Calyx*** tubular, 20–25 mm long, more or less evenly 5-lobed, lobes triangular, 5 mm long, hairy externally. ***Corolla*** pale pink, 23–30 mm long, barely longer than the calyx, curved and slightly swollen below the throat, lobes unequal, upper lobes much smaller, sparsely hairy externally. ***Stamens*** with filaments 3–4 mm long, curved.; anthers 2 mm long, connected at apices before dehiscence; staminodes 3, c. 1 mm long. ***Gynoecium*** c. 15 mm long (damaged at base); disc not seen; ovary not seen; style glandular at the top of the style near the stigma, glabrous towards the ovary; stigma bilobed, lobes vertical, possibly immature, 2 mm long, densely glandular on inner surface of lobes. ***Fruits*** ovoid, 10-11 mm x 6-7 mm, glabrous, calyx and base of style not persistent.

Distribution. North Sulawesi (Fig. 2.56).

Habitat and ecology. Upland forest at an altitude of 1100–1500 m.

Etymology. This species is named after its unusual spicate inflorescence (de Vriese, 1856).

Proposed IUCN conservation category. This species has an EOO of 88 km^2 and an AOO of 12 km^2 based on 2 km x 2 km grid cell size under the B criteria (Bachman et al., 2011). (map in Appendix 2.1). There are no protected areas in the distribution range of this species (UNEP-WCMC & IUCN,

2019) which is close to one of the most populated areas of Sulawesi where threats from intensive agriculture and urban expansion are known (Cannon et al., 2007); the number of collections are low and there are no collections more recent than 1895 despite relatively frequent fieldwork in North Sulawesi. It is suggested that this species is considered Critically Endangered under the criteria B1b.

Additional specimens examined: **North Sulawesi:** Minahassa, Koleskai, G. Masarang**,** 10 i 1895, *Koorders* 17197 (BO, L); Koles-kai, G. Lokon, 7 i 1895, *Koorders* 17203 (BO, L).

Sulawesi Group: 7 (Atkins et al., Chapter 3).

Notes. This species, with its pendulous, spicate inflorescence, is very distinctive, most similar to the widespread *C. celebica* with its cauliflorous, but more open and branching, inflorescence. It can most easily be distinguished vegetatively from this species by leaf shape and venation with the leaves of *C. spicata* being oblanceolate with decurrent leaf bases and 7-9 pairs of lateral veins and those of *C. celebica* being ovate, not decurrent and with up to 19 lateral vein pairs.

The description for *C. spicata* is brief as the material available is not complete and has been compiled to a large extent from de Vriese's original description and illustration and a single damaged flower. In all specimens seen, the inflorescences have become detached but it appears from the original illustration as if they are pendulous from the branches or possibly in the axils of fallen leaves.

Reinwardt's collection from November 1821, and bearing the description, 'in sylvis montis Klabat' and annotated with the manuscript name '*Rhynocarpus spicatus'* is selected here as the Lectotype.

Koorders 17197 and 17203 have both been annotated with the herbarium name of *C. cauliflora* Koord. sp.nov. but are later determined by Koorders as *C. spicata* de Vriese. Koorders never published the name *C. cauliflora* and Merrill uses it later for an unrelated Philippine species (Merrill, 1920).

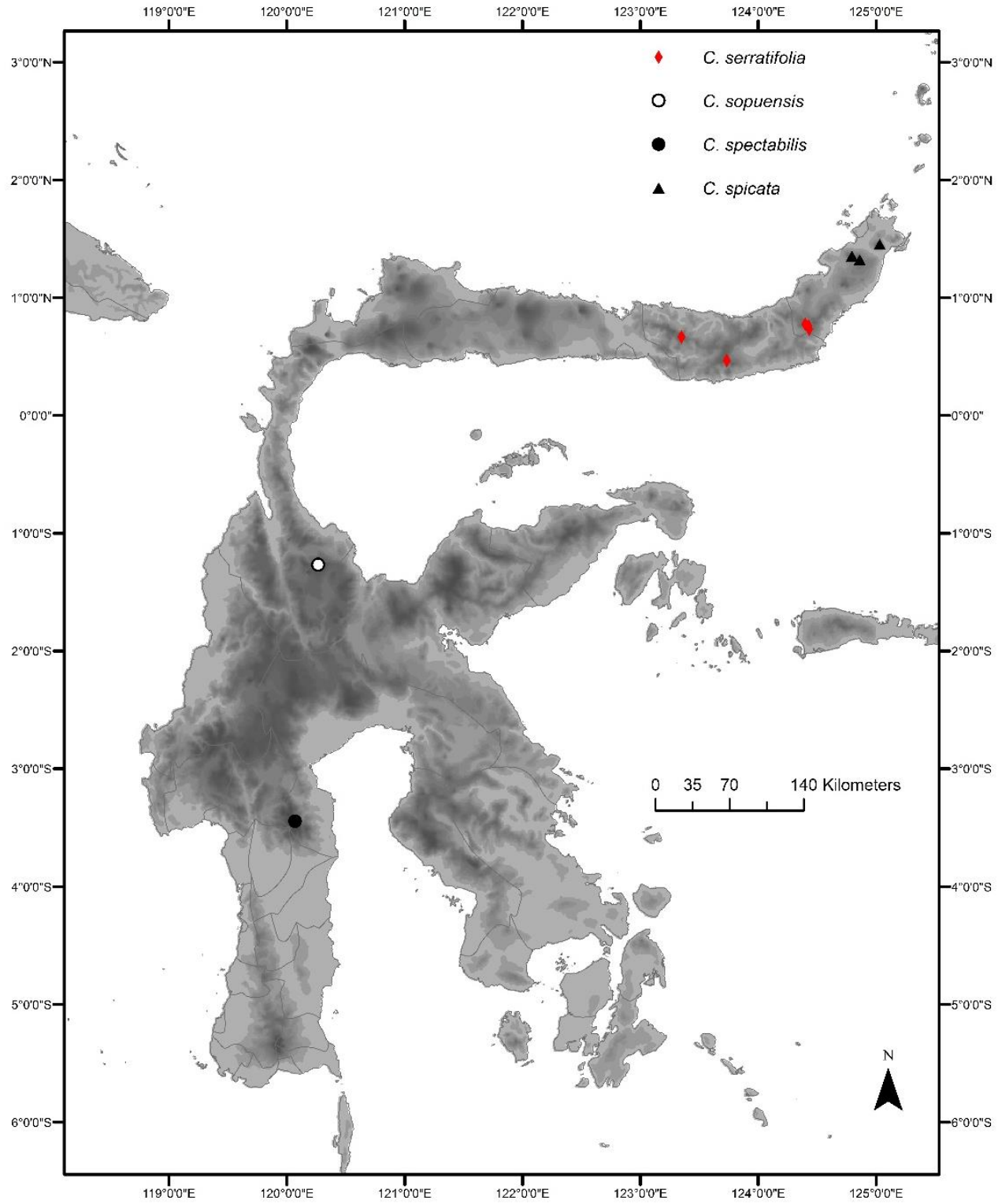


Fig. 2.56 Distribution of *Cyrtandra serratifolia* (red diamonds), *C. sopuensis* (white circles), *C. spectabilis* (black circles) and *C. spicata* (black triangles).

Cyrtandra sulcata Blume, Bijdr. 14: 770 (1826) - Type: Java, *Blume* 221 (lectotype L hic desig.).

Shrub (height not recorded)***. Stems*** striate, somewhat grooved, densely hairy on young growth, almost glabrous on older growth. ***Leaves*** opposite, both members of a pair well developed but unequal in size; petiole very variable, 7–70 mm long, hairy; blades 14–30 x 4–10 cm, narrow oblong to narrow obovate, apex acuminate, base attenuate, slightly unequal, margin serrulate to serrate; 9–14 pairs of lateral veins and reticulate tertiary venation, sparsely hairy above and below, more densely so on midrib and veins. ***Inflorescences*** axillary, subsessile, with up to 6 flowers at various stages of development; bracts narrow ovate, 6–7mm x 3–5 mm, densely hairy; peduncles 3—4 mm long, sparsely hairy. ***Calyx*** 10 mm long, two lower lobes 5.5 mm long, long acuminate, three upper lobes slightly shorter, long acuminate, 4.5 mm long, densely hairy externally. ***Corolla*** white, slightly purplish in bud, 14 mm long, more or less parallel-sided, widening very gradually to mouth, mouth oblique, lower lip somewhat extended, hairy externally and with glandular hairs internally on lobes and mouth. ***Stamens*** with filaments 3.5 mm long, attached 8 mm from base of corolla, glabrous; anthers 1 mm long, glabrous; staminodes not seen but corolla damaged. ***Gynoecium*** 7 mm long; disc unilateral with very slightly lobed margin, 1.5 mm long, glabrous; ovary and style densely hairy; stigma slightly bilobed, 1.5 mm across. ***Fruits*** ovoid, drying dark brown, hairy, particularly towards base of persistent style, verrucose, 5–10 x 3–4 mm, base of style and calyx persistent.

Distribution. South Sulawesi (Fig. 2.59).

Habitat and ecology. Lowland, hill and upland forest at an altitude of 50-1400 m.

Etymology. This species is named for its grooved stem and branches (Blume, 1826).

Proposed IUCN conservation category. This species is recorded from Sulawesi, Java (Bakhuizen van den Brink, 1950) and Sumatra (fide Bakhuizen K, L) and appears to be one of the most widespread *Cyrtandra* species in the region. The collections in Sulawesi, however, are from the densely populated area around Makassar at relatively low altitude primarily in lowland and hill forest which is the most threatened on the island (Cannon et al., 2007) and outside of any protected areas (UNEP-WCMC & IUCN, 2019). No collections have been made of this species since 1976 despite this area

being very accessible. Based on the distribution of the species in Sulawesi, the EOO is 572 km^2 and the AOO is 16 km^2 based on a 2 x 2 km grid cell size (Bachman et al., 2011) (map in Appendix 2.1). Given the multi-island distribution of this species, however, we consider it to be Least Concern.

Additional specimens examined: **South Sulawesi.** Lombasang, 25 iv 1921, *Bünnemeyer* 11164 (BO,L); ibid, 29 iv 1921, *Bünnemeyer* 11233 (BO); ibid, 25 v 1921, *Bünnemeyer* 11734 (BO, L); G. Bonthari(?), 28 v 1921, *Bünnemeyer* 11766 (BO, L); Not legible, 1 vii 1921, *Bünnemeyer* 12608 (BO); Bantimoemoeroeng, 20 ii 1938, *Buwalda* 3798 (BO, K, L); NE of Makassar, within 54-60 km on the road, 5 vii 1976, *Meijer* 10881 (A, BO, L, MO, S); Tjamba, Not legible, *Teysmann* 12641 (BO).

Sulawesi Group: 9 (Atkins et al., Chapter 3).

Notes. This species is similar to *C. longirostris* from North Sulawesi in being a shrub with subequal leaves and axillary inflorescences with small white flowers, ovoid fruits and narrow inflorescence bracts but can be most easily distinguished from this species by its much shorter peduncles (3—4 mm long vs 15—40 mm long) as well as its densely hairy, as opposed to glabrous, ovary and unilateral, as opposed to cupular, nectary disc.

Cyrtandra sulcata was first described by Blume from Java and has a distribution that includes Sumatra (fide Bakhuizen, L) and, now, Sulawesi. The description here is based on the Sulawesi collections only. The Sulawesi material is a good match for the type from Java and shows the key diagnostic characters of non-decurrent leaf bases, a unilateral disc and densely hairy ovary (Bakhuizen van den Brink, 1950).

Blume did not designate a type when he described this species so a Blume collection from Java, listed by Clarke (1883) under this species in his monograph but not formally lectotypified is selected here as the lectotype.

Cyrtandra tenuicarpa H.J.Atkins, Edinburgh J. Bot. 60(3): 316 (2004). – Type: Sulawesi, Road between Palopo and Rantepao, 3 iii 2000, *Mendum* et al. 00229 (holotype BO; isotype E). **Fig. 2.57**

Branching herb to 1.2 m in height. ***Stems*** striate, sparsely hairy, more densely so when young. ***Leaves*** opposite, both in each pair well developed but somewhat unequal; petiole 4–8 mm long, hairy; blades (6–)8–14 cm × 3–6 cm, elliptic, apex acuminate, base attenuate and strongly asymmetric, margin subentire to minutely serrulate; 10–12 pairs of lateral veins curving upwards, sparsely hairy above and below, more densely so on midrib and veins. ***Inflorescences*** axillary, pedunculate and pendulous, 3–5–flowered; bracts 1–2 mm long, ovate, hairy to densely hairy; peduncles 35–80 mm long, sparsely hairy, slender (0.5 mm diameter); pedicels 7–15(–30) mm long. ***Calyx*** pale green, 4–5 mm long, slightly bilabiate, 5-lobed, lobes triangular, acuminate, 2–3 mm long, sparsely hairy externally. ***Corolla*** white,15–16 mm long, narrow below, widening to mouth apically, upper lobe larger than others c. 5 × 3 mm, other lobes smaller, somewhat recurved, c. 2 × 2 mm, glandular hairy externally. ***Stamens*** with filaments 4–5 mm long, attached 10 mm from base of corolla; anthers 1 mm long, not cohering at apices before dehiscence; staminodes 3, less than 1.5 mm long. ***Gynoecium*** 14–15 mm long; disc cupular, undulate, 1 mm long, glabrous; ovary and style glandular-hairy; stigma bilobed, lobes vertical and pressed together, oblong, 1 mm long. ***Fruits*** linear, 25–35 mm × 1.5–2 mm, green when young, glabrous except for glandular hairs on persistent style, calyx sometimes persistent.

Distribution. South, West and Central Sulawesi (Fig. 2.59).

Habitat and ecology. Upland and montane forest at an altitude of 800-1642 m.

Etymology. This species is named for its distinctive, narrow fruits (Atkins, 2004).

Proposed IUCN conservation category. It has not been possible to trace the exact locality of *Rachmat* 573 so the EOO and AOO are based on three of the four known collections. The EOO is 314 km^2 and the AOO is 12 km^2 based on a 2 x 2 km grid cell size (Bachman et al., 2011) (map in Appendix 2.1). The collections are from areas of upland and montane forest which are slightly less threatened than the lower altitude forest (Cannon et al., 2007) but none of the collections for which we have accurate location information are from protected areas (UNEP-WCMC & IUCN, 2019). A category of

Vulnerable is suggested for this species under the criterion VUD2 to reflect the low number of collections and lack of any formal protection.

Additional specimens examined: **Central Sulawesi**. Gunung Timbaang, 1913, *Rachmat* 573 (BO);
West Sulawesi. Mamasa Regency, Gunung Gandang, 20 iv 2016, *Kartonegoro, Ardiyani, Santoso & Wulansari* ARK 902 (BO, E);
South Sulawesi. Todjamboe, 800 m, 20 vi 1929, *Kjellberg* 1686 (BO, S).

Sulawesi Group: 13 (Atkins et al., Chapter 3).

Notes. C. tenuicarpa is distinctive in Sulawesi, identified most easily by its very narrow fruits. This is a character much more commonly seen in Borneo, in species such as *C. elmeri* Merr*., C. dallasensis* B.L.Burtt and *C. bullifolia* B.L.Burtt.

A note on the *Kartonegoro* et al. ARK902 collection from West Sulawesi states that it is used for fever medicine.

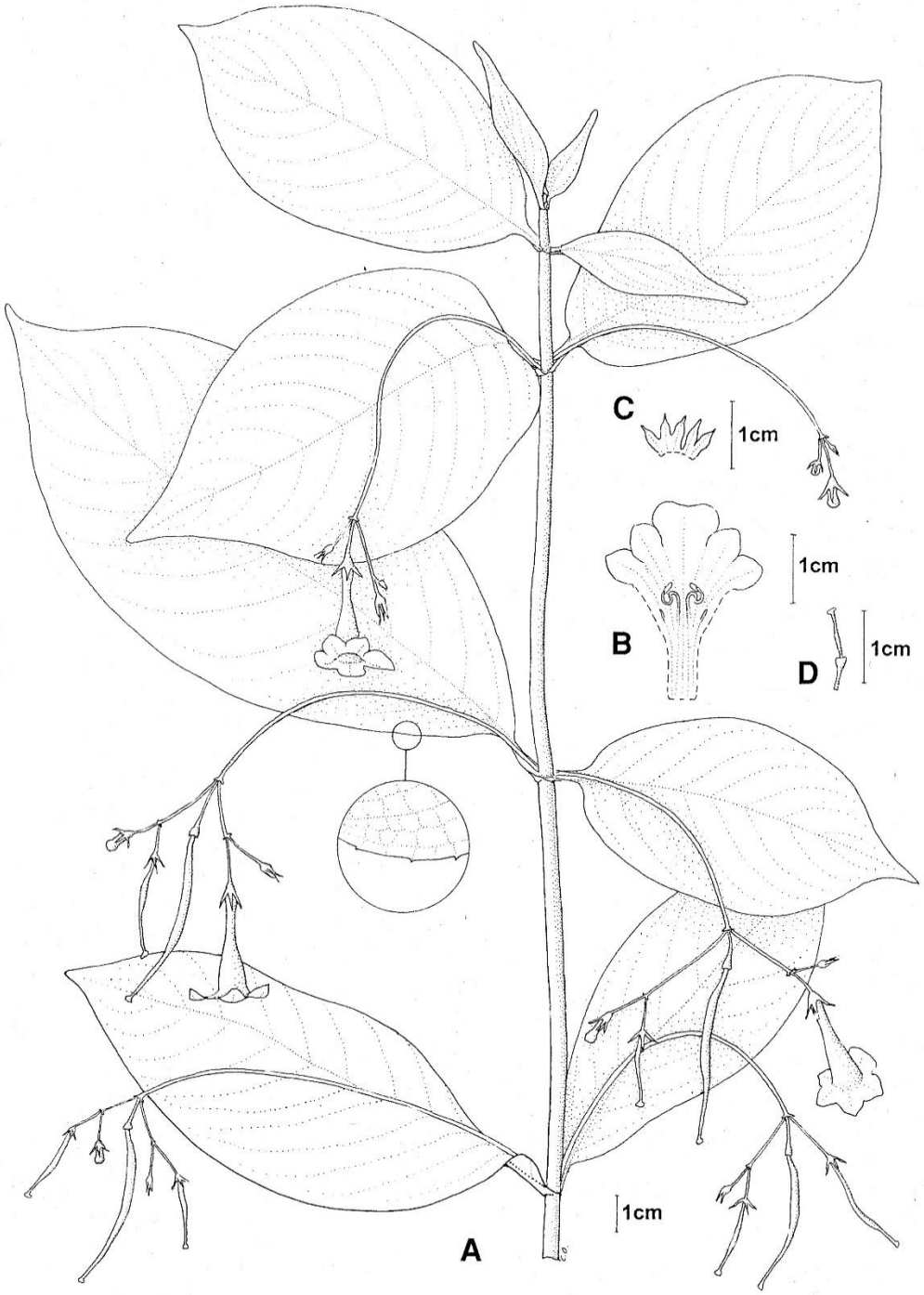


Fig. 2.57 Line illustration of *Cyrtandra tenuicarpa* showing a. Habit b. Opened corolla showing position of stamens and staminodes c. Opened calyx showing inner surface d. Gynoecium including disc. Drawn by Christina Oliver from Mendum et al., 00229. Reproduced from Atkins (2004).

Cyrtandra widjajae Karton., Reinwardtia 14(1): 6 (2014) – Type: Sulawesi, Mekongga Mts, North Kolaka, Rante Angin District, Tinukari Village, 28 xi 2010, *Widjaja* et al. 9412 (holotype BO; isotypes DAV, E). **Fig. 2.58**

Shrub to 2m in height. ***Stems*** striate, sparsely hairy. ***Leaves*** opposite; one leaf of a pair markedly reduced; petiole 5–10 mm long, glabrous to sparsely hairy; blades of larger leaves 7–16 × 2–4 cm, narrow oblong to oblanceolate, apex long acuminate, acute at base, slightly asymmetrical; subentire with 8–14 pairs of lateral veins, curving upwards and running out to margin, subglabrous above, sparsely hairy below, more densely so on midrib and veins. *Reduced leaves* 5–10 mm × 5–7 mm, ovate to cordate, resembling the larger leaves in other respects. ***Inflorescences*** axillary, subsessile, 1–4(—7)-flowered; bracts 2—4 mm × 0.5—1 mm, linear, hairy; pedicels 2–4 mm long, sparsely to densely hairy. ***Calyx*** narrow campanulate, white to pale green, 6–10 mm long, more or less evenly 5-lobed to slightly bilabiate with three upper lobes united into a shallowly triangular lip and two lower lobes mostly free, lobes linear, 3-7 mm long, sparsely hairy externally. ***Corolla*** white, 12–15 mm long, tube narrow in basal half, gradually widening to mouth in upper half, upper lobes 2—4 mm x 1—2 mm, lower and lateral lobes 3-5 mm x 1-2 mm, hairy externally, glandular hairy internally on the lobes, particularly towards the base and inside tube below the anthers. ***Stamens*** with filaments 3–5 mm long, attached 5–6 mm above base of corolla, glabrous; anthers 1—1.5 mm long, cohering at apices before dehiscence; staminodes tiny, c. 1 mm long. ***Gynoecium*** 6–9 mm long; disc cupular with lobed margin, 1 mm long, glabrous externally; ovary densely eglandular hairy; style densely eglandular hairy becoming glandular towards stigma; stigma bilobed, 1—1.5 mm across. ***Fruits*** 8–13(—30) mm × 2–3(—5) mm, oblong and often curved, densely hairy, calyx not or only partially persistent, base of style persistent.

Distribution. North, Central and South East Sulawesi. (Fig. 2.59).

Habitat and ecology. Lowland, hill and upland forest at an altitude of 300 to 1100 m.

Etymology. This species is named after Elizabeth A. Widjaja (BO), bamboo taxonomist and one of the collectors of the type of this speices (Kartonegoro & Potter, 2015).

Proposed IUCN conservation category. The EOO of this species is 102,193 km^2 and the AOO is 44 km^2 based on a 2 x 2 km grid cell size (Bachman et al., 2011) (map in Appendix 2.1). Some of the collections in the northern area of the distribution fall within the limits of the Bogani Nani Wartabone National Park and both of the collections in Central Sulawesi fall within Lore Lindu National Park (UNEP-WCMC & IUCN, 2019) so will have some degree of protection but none of the collections in the southern population are protected and most of the collections are from the more threatened lowland and hill forest areas (Cannon et al., 2007). A category of Least Concern is given for this species

Additional specimens examined: **North Sulawesi**. Bolaang Mongondow, Mt London, near Tunpa river, 31 xi 2016, *Barber, Atkins, Kartonegoro & Kinho* BAKK32 (BO, E); Dumoga Bone National Park, 5 i 1996, *Kato, Okada, Setoguchi & Darnaedi* 355 (L); Minahassa, Pinamorongan, 30 i 1895 *Koorders* 17192B (BO, L); Bolaang Mongondow, 7 iii 1985, *de Vogel & Vermuelen* 6779 (E, L); 1 iv 1985, *de Vogel & Vermeulen* 6829 (E, K, L); 220 km W of Menado, 7 iii 1990 *Burley* et al. 3697 (A, CANB, K, L, SING);
Central Sulawesi. Sopu Valley, 29 iv 1979, *Hennipman* 5115 (BO, L); Mt Roroka Timbu, w. slope, 11 v 1979, *de Vogel* 5278 (BO, L, NSW);
South East Sulawesi. Along the trail to Mekongga Mt, 19 iii 2006, *Girmansyah* 596 (BO); Along Uwitalambeh River, near Mt Pobindaa omanu, west of Wutamole, 17 v 2008, *Girmansyah* 941 (BO); Tawanga, B. Watoewila, 25 iii 1929, *Kjellberg* 983 (BO).

Sulawesi Group: 14 (Atkins et al., Chapter 3).

Notes. Cyrtandra widjajae is part of the group of seven species that share the characters of strongly anisophyllous leaves; white or light yellow corollas and densely hairy calyces, corollas and fruits. The others in the group are *C. gambutensis, C. gorontaloensis, C. balgooyi, C. engleri, C. parvicalyx* and *C. sopuensis.* This species was first described from the under-collected Mekkongga region of South East Sulawesi (Kartonegoro & Potter, 2015). Included here under *C. widjajae* are a group of specimens from Minahassa and Bolaang Mongondonow in North Sulawesi. These collections had originally been given the herbarium name *Cyrtandra minahassae* by Koorders and this name was included in a list of *Cyrtandra* species present on the island but a description was never provided (Koorders, 1898). It seems that Koorders changed his mind about the distinctiveness of this species as his

original collection of *C. minahassae* (*Koorders* 17192B) was later re-determined by him as *C. engleri.* Further discussion of the differences between *C. engleri* and *C. widjajae* are given under that species.

In addition to these two disjunct groups there are two collections from Central Sulawesi, from the Sopu Valley, that are included here more tentatively; *Hennipman* 5115 and *de Vogel* 5278, have fewer lateral veins on the leaves and slightly larger flowers. Further collections from throughout its distribution, but particularly from Central Sulawesi, are required to clarify the limits of this species and the extent of variation.

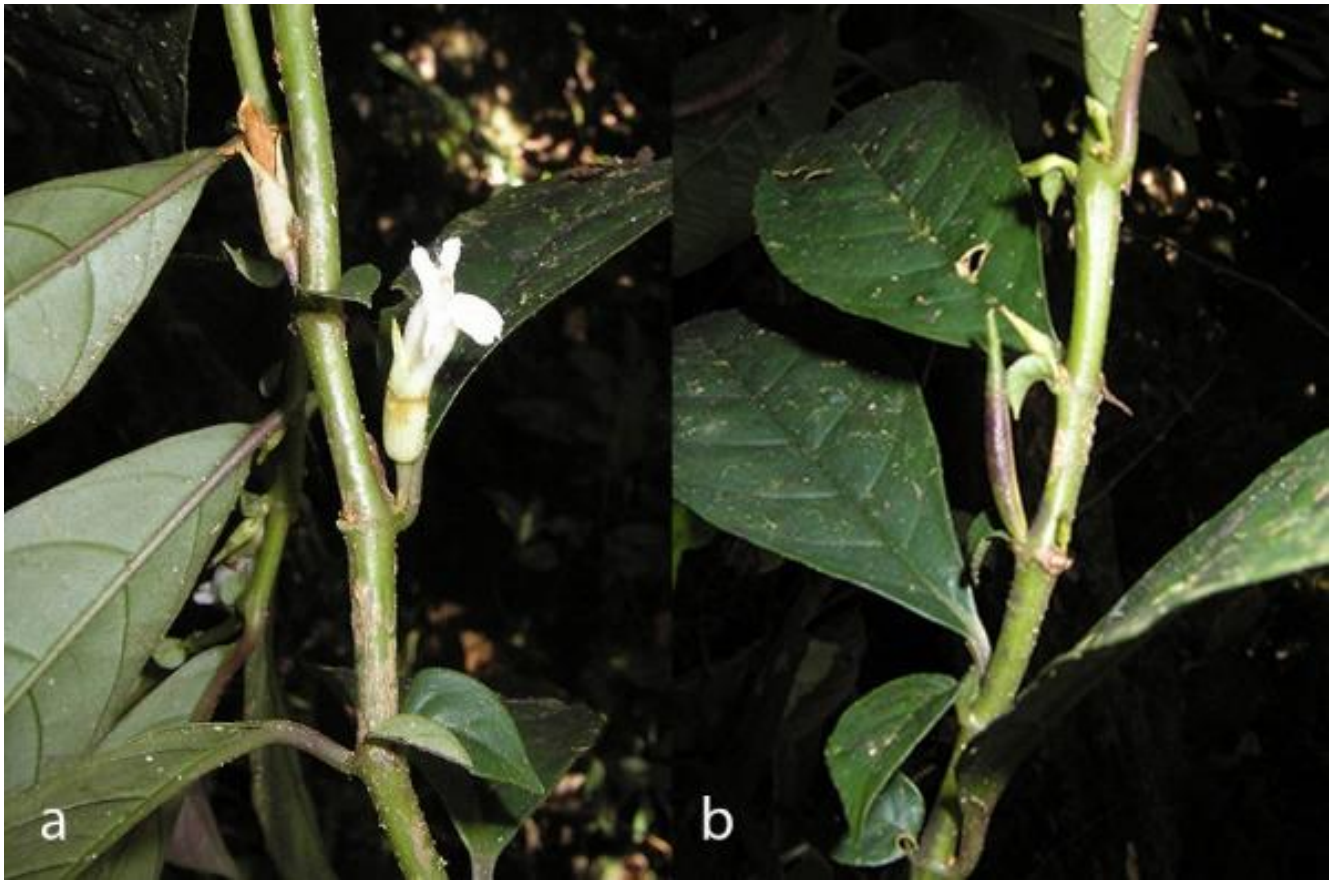


Fig. 2.58 Plate of *Cyrtandra widjajae* showing a. side view of corolla b. fruit. Widjaja et al. 9412. Photos: D. Girmansyah.

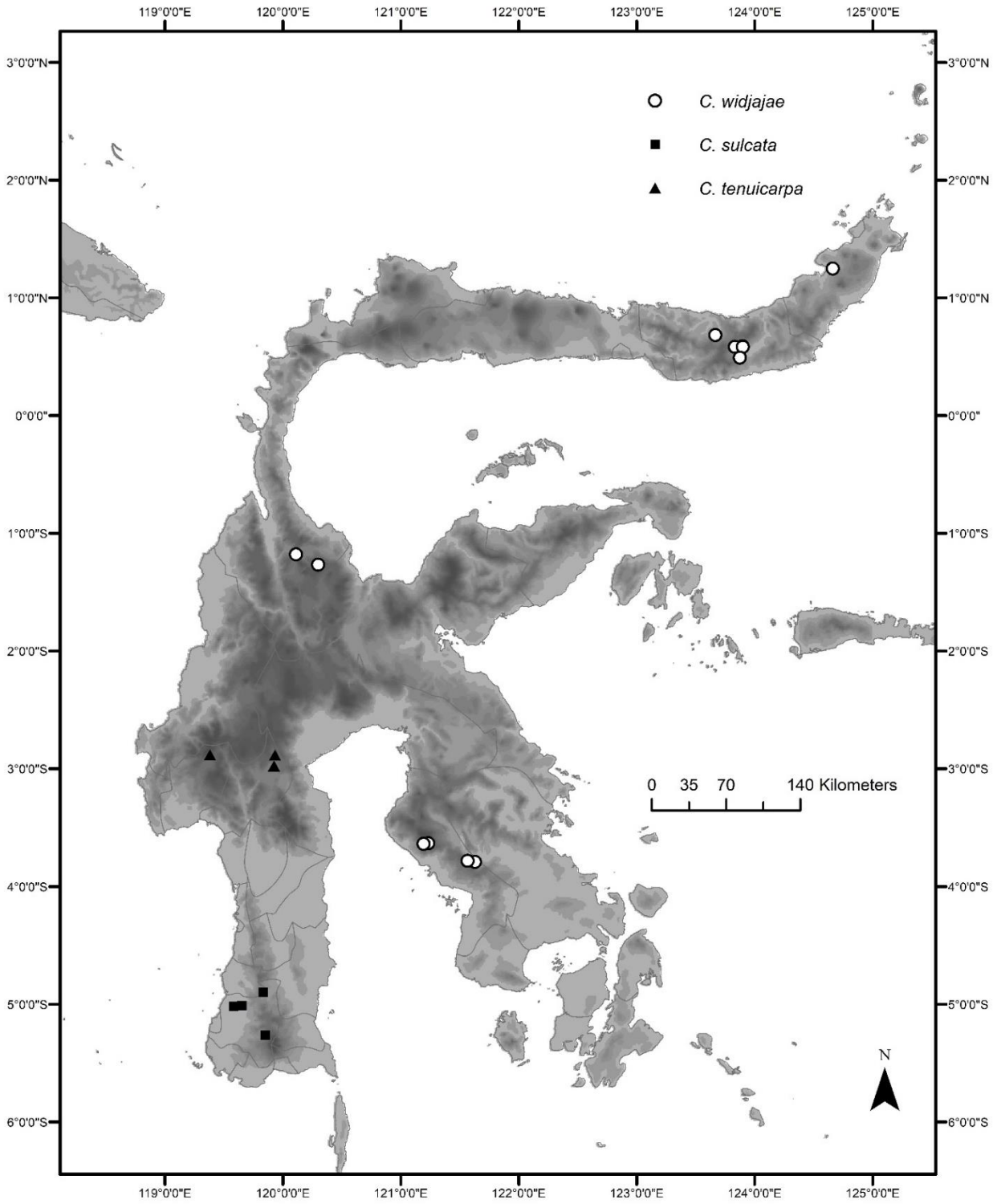


Fig. 2.59 Distribution of *Cyrtandra sulcata* (black squares)*, C. tenuicarpa* (black triangles) and *C. widjajae* (white circles).

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ACKNOWLEDGEMENTS

We would like to thank the curators of the following herbaria for loan of material or access to their collections: A, BM, BO, CANB, E, K, KRB, L. We are grateful to Christina Oliver and Claire Banks for their excellent illustrations; to Deden Girmansyah, Wisnu Ardi and Sadie Barber for the inclusion of their photographs and to Steve Scott, Sadie Barber, Nathan Kelso and Stephen Willis for taking excellent care of the living collections of *Cyrtandra* at RBGE. We would also like to thank the staff of the Kebun Raya and Bogor herbarium for their assistance in the field, especially Hendrian and Sofyan, and Julianus Kinho from the Menado Institute of Forestry. We would also like to thank the following for general advice and comments on the manuscript: Sandy Atkins, Mark Coode, David Middleton, Mark Hughes and Peter Wilkie. Finally, we would like to thank the Edinburgh Botanic Garden (Sibbald) Trust and the Singapore Botanic Garden Fellowship for funding aspects of this research.

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Appendix 2.1. Geospatial analysis of Sulawesi *Cyrtandra* for provisional conservation assessments using GeoCAT online assessment tool http://geocat.kew.org/. All species listed alphabetically. No map for *C. sandei*.

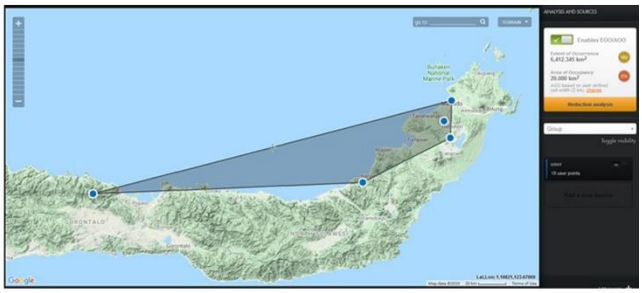
C. albiflora

C. balgooyi

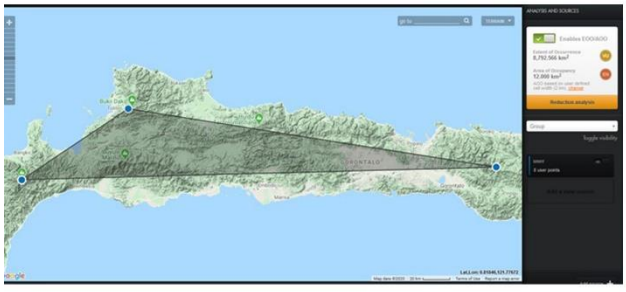
C. boliohutensis

C. bruteliana

C. celebica



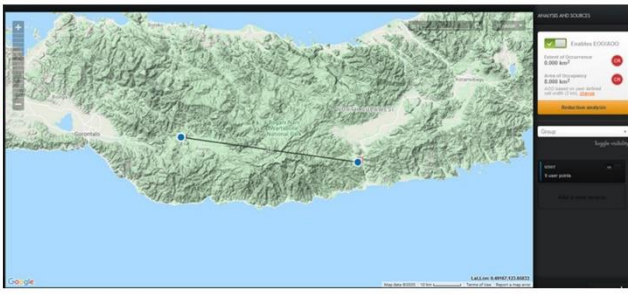
C. engleri



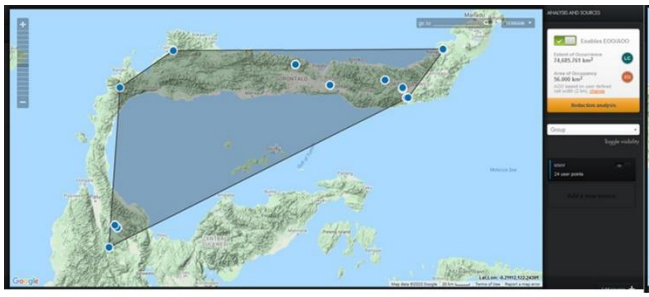
C. fasciata

C. flavomaculata

C. floccosa

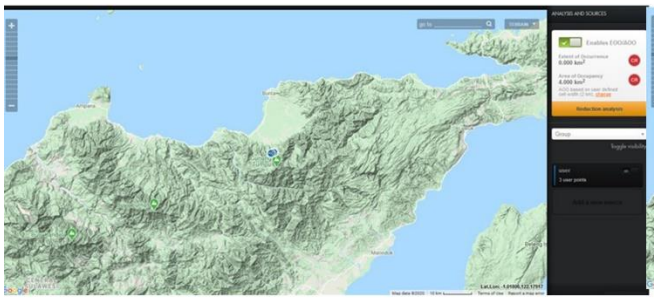


C. gambutensis



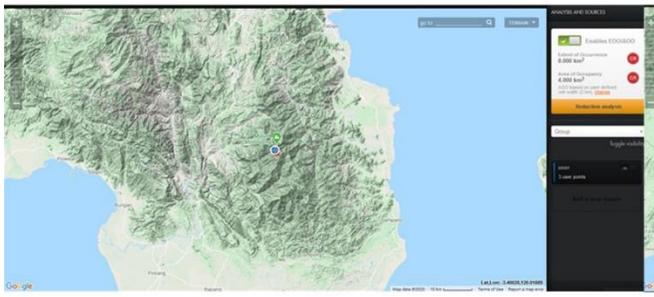
C. geocarpa

C. gorontaloensis

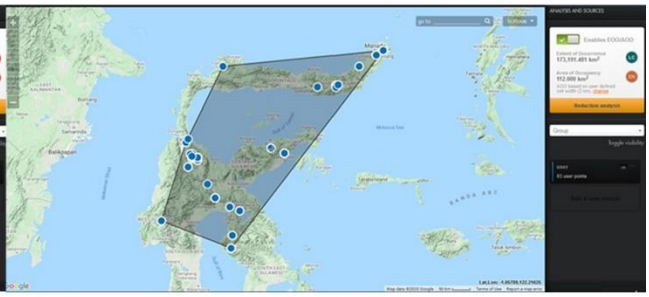


C. hekensis

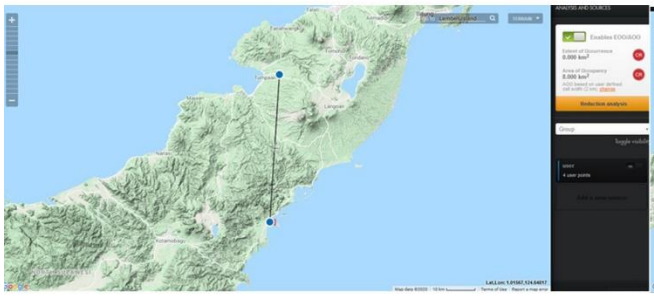
C. hendrianii



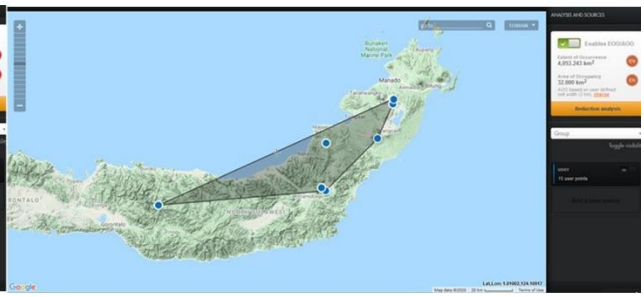
C. hispidula



C. hypogaea



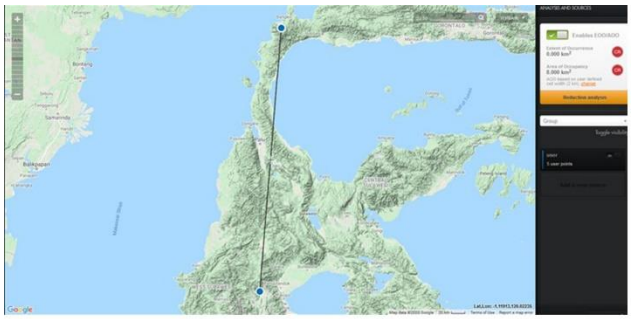
C. jellesmani



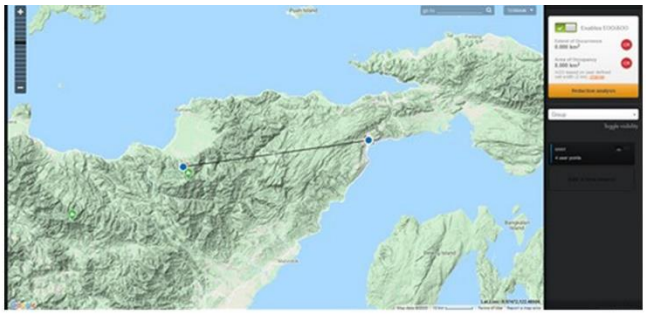
C. kinhoii

C. kjellbergii

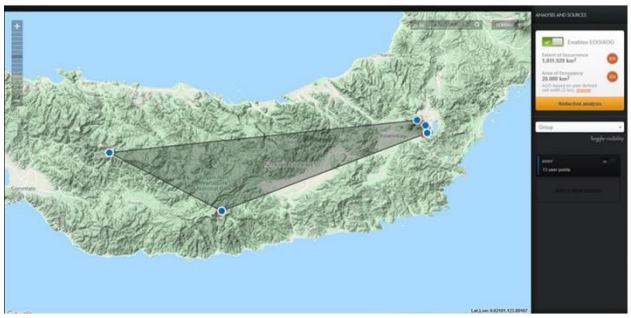
C. longirostris



C. roseiflora



C. rubribracteata



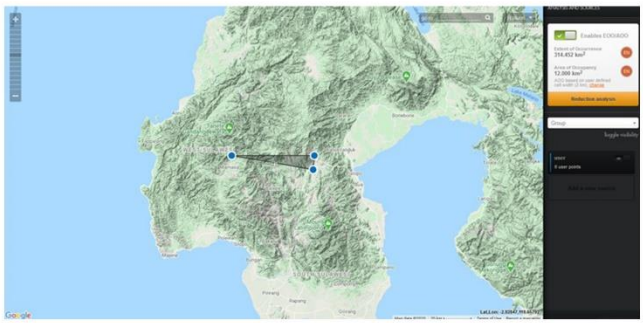
C. serratifolia

C. sopuensis

C. spectabilis

C. spicata

C. sulcata



C. tenuicarpa

C. widjajae

Chapter Three: A molecular phylogeny of southeast Asian *Cyrtandra*: confirmation of morphological homoplasy and sectional polyphyly and options to facilitate future taxonomy of the genus in the region

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Abstract

A well sampled molecular phylogeny of southeast Asian *Cyrtandra* and subsequent optimisation of selected morphological characters has allowed us to develop a strategy for tackling this large genus taxonomically in the absence of a functional infrageneric system. The poor morphological diagnosability of the six major clades resulting from the homoplasy of macromorphological characters, combined with some degree of floristic exchange between islands, suggests that a single approach, based on geography, morphology or phylogeny, will not be satisfactory for *Cyrtandra* and that an integrative method, as demonstrated in other large genera, would be most appropriate. We assessed the integrative method outlined in Clark et al. (2013)'s concept of phylogenetically informed revisions of restricted geographic areas on the *Cyrtandra* species of (i) Sulawesi and (ii) Borneo and found it to be a promising approach. This study has defined 28 groups based on a combination of phylogenetics, geography and morphology.

Keywords

Infrageneric classification, large genera, character optimisation,

3.1 Introduction

Large genera present considerable challenges to the taxonomist due to their sheer size and they have often been neglected for this reason, becoming taxonomic 'black holes' (Moonlight et al., 2018) where species boundaries are uncertain and many new species await description. It is crucial, however, that they are tackled in order to fully understand evolutionary dynamics and speciation in these highly successful groups and for their potential contribution to related fields including

conservation and biogeography to be realised (Bramley, 2003; Frodin, 2004; Moonlight et al., 2018). The sheer size of these genera make it difficult for a single taxonomist to monograph them completely within a career and, in these cases, it is necessary for the genus to be divided in order to delimit more manageable taxonomic studies of smaller units, which enables a team approach (Bramley, 2003; Frodin, 2004; Knapp, 2008; van Welzen et al., 2009; Lucas et al., 2011; 2018). The advantages of an infrageneric classification based on phylogenetic principles and supplemented by morphological data in an integrative approach are well documented (Bramley, 2003; Frodin, 2004; Moonlight et al., 2018; Legume Phylogeny Working Group, 2013; Lucas et al., 2011; 2018; Nic Lughada et al., 2019).

Cyrtandra is the largest genus in the Gesneriaceae with over 800 species of herbs, shrubs and occasionally trees (Burtt, 2001; Atkins et al., 2013). Centres of diversity for the genus are Borneo (c.200 spp.), the Philippines (c.150 spp.), and New Guinea (c.120 spp.) (Atkins et al., 2013). Approximately 175 species are also distributed across the Pacific Basin. Most species are narrow endemics with few examples of widespread species (Atkins et al., 2013). *Cyrtandra* is found predominantly in the rainforest, from sea level to 3000m (Burtt 2001, Atkins et al. 2013). This high diversity, large number of endemic species, and wide distribution make it an ideal genus for examining biogeographic patterns (Atkins et al. 2001, Cronk et al. 2005, Clark et al. 2009, Johnson et al. 2017) and investigating the processes which underlie current patterns of biodiversity (Bramley et al. 2004, Johnson et al. 2015, 2019). Its sheer size also poses major taxonomic challenges, since there is currently no effective infrageneric classification, greatly increasing the difficulty of working with the group and hampering the planning of future taxonomic work (Burtt, 2001; Bramley, 2003; Atkins et al., 2013).

The only taxonomist to attempt a classification system for *Cyrtandra* across its distribution was Clarke (1883). Working with far fewer specimens than are now available, he recognised 164 species of *Cyrtandra,* which he divided into two subgenera and thirteen sections. Subsequently, and due to shortcomings in Clarke's system, two additonal sectional classifications were developed based on geographic subsets: one for Hawaiian *Cyrtandra* (Hillebrand, 1883) and one for the genus in New Guinea (Schlechter, 1923).

The only integrative approach combining both molecular and morphological data undertaken so far was by Clark et al. (2013) for the Solomon Islands. They produced a phylogenetically informed revision of *Cyrtandra* on the Solomon Islands arranged according to the four lineages present on the island. These lineages were revealed by their inclusion in a wider phylogeny of *Cyrtandra* in the Pacific. The lineages were then characterised morphologically and a key to the lineages provided.

Crucially, integrating morphology also allowed those species from the Solomon Islands that had not yet been sequenced to be placed in to one of those four lineages. Clark et al. (2013) proposed that phylogentically informed revisions of a geographic area are a proof of concept that might be useful for *Cyrtandra* more widely.

Developing an approach for tackling *Cyrtandra* based on phylogenetic principles and supplemented by morphological data is of critical importance for future studies in the genus (Nic Lughada et al., 2019). Molecular and morphological data for *Cyrtandra* has been most notably lacking from the southeast Asian region and we aim here to provide a well sampled phylogeny of *Cyrtandra* across southeast Asia, to complement ongoing work on the genus in the Pacific, and to use the phylogeny to:

1. Evaluate the genus-wide infrageneric system in a phylogenetic context
2. Test a selection of key macromorphological characters to determine their degree of homoplasy and to assess their suitability to diagnose any future infrageneric classification
3. Test Clark et al. (2013)'s concept of a phylogenetically informed revision of a geographic area on two species-rich islands in southeast Asia:
    a. In Borneo, an island with approximately 200 *Cyrtandra* species (Atkins et al., 2013), great morphological diversity (Burtt, 2001) and for which taxonomic work and plant identifications are severely hampered by the lack of a key or synthesis of existing information.
    b. In Sulawesi, an island of 40 species where the taxonomy is well documented (Chapter Two).

We conclude by reviewing options for facilitating future taxonomic research in *Cyrtandra.*

3.2 Methods

3.2.1 Taxon sampling

We sampled a total of 192 accessions representing 128 *Cyrtandra* species (Table 1). Six species from within the Didymocarpinae (the same subtribe as *Cyrtandra*) were selected as outgroups (*Aeschynanthus roseoflorus, A. buxifolius, Agalmyla chalmersii, Didymocarpus antirrhinoides* and *Loxostigma griffithii*). These allowed a robust test of the monophyly of *Cyrtandra* but were closely related enough to allow unambiguous alignment of the DNA sequence data. We applied names to as many of the samples as possible, including 20 new species, which were published partly based on

our phylogenetic evidence: sixteen from Sulawesi (Kartonegoro et al., 2018; Chapter Three); two from New Guinea (Atkins et al., 2019), one from Sumatra (Smith et al., accepted) and one from the Philippines (Olivar et al., in press) (published papers included in the Appendix) but much taxonomic work is still required and many of the samples may represent undescribed species. We included a number of taxa named only to genus level (13 samples representing 13 taxa), or with some degree of affinity to a known species (as aff. or cf.) (21 samples representing 16 taxa). In addition to covering a wide geographic area, we tried to cover as much of the morphological variation in the genus that we could, covering as many of the existing infrageneric divisions. Full details of Clarke's sections (1883) are given in Appendix 3.1 with a list of the species in this study which are referrable to those sections.

3.2.2 Molecular methods

The methods used here follow those detailed in Atkins et al. (2020). Total genomic DNA was extracted from fresh leaf material or silica dried material using a modified CTAB procedure (Doyle & Doyle, 1987) or using the Qiaxtractor (Qiagen, Hilden). One nuclear (ITS) and four chloroplast regions (*mat*K, *trn*L-F, *psb*A-*trn*H and *rpl*32-*trn*L) were sampled. PCR was carried out with Biotaq DNA polymerase (Bioline, London) and with CES PCR enhancer (Ralser et al., 2006) with the following chemical concentrations (10× buffer 1µl, 20mM dNTP 1 µl, 50 mM $MgCl_2$ 0.3 µl, forward and reverse primers 0.4 µl each, CES 2 µl, Biotaq 0.2 µl, DNA 1 -2 µl and H_2O added to make up 10 µl). PCR amplifications were carried out under the following conditions: ITS and *mat*K: 94°C for 4 min, 35 cycles of 94°C for 1 min, 55°C for 1 min, 72°C for 1.5 min, followed by 72°C for 10 min; *trn*L-F: 94°C for 4 min, 35 cycles of 94°C for 30 seconds, 57°C for 30 seconds, 72°C for 1 min, followed by 72°C for 10 min; *psb*A-*trn*H and *rpl*32-*trn*L: 94°C for 4 min, 35 cycles of 94°C for 1 min, 52°C for 1 min, 72°C for 1.5 min, followed by 72°C for 10 min. All PCR amplifications were carried out on a Bio-Rad Tetrad DNA Engine (Bio-Rad, Hercules, CA). The PCR products were visualised under UV light after electrophoretic separation on a 1% agarose gel stained with SYBR Safe gel stain (Invitrogen, Carlsbad, CA). PCR products were subsequently purified using ExoSAP-IT (Thermo Fisher Scientific, Waltham, MA) following the manufacturer's protocol. PCR products were sequenced using the BigDye™ Terminator v 3.1 Cycle Sequencing Kit (Applied Biosystems™, Foster City, CA) following the manufacturer's protocol, with the same primers used for PCR amplification. Sequencing was carried out by Edinburgh Genomics at the University of Edinburgh. The resulting electropherograms were combined and edited in Sequencher v 5.1 (Gene Codes Corporation, Ann Arbor, MI) and a matrix assembled, aligned and manually adjusted in Bioedit v 7.1.11 (Hall, 1999).

3.2.3 Phylogenetic analyses

Maximum Parsiomony (MP) analyses were conducted on individual regions to assess congruence visually, with areas of conflict determined by examining the placement of individual taxa on each gene tree. Relationships were considered incongruent if the placement of taxa varied among the individual gene trees and exhibited MP-BS values > 80%. In order to further examine incongruence between the datasets an Incongruence Length Difference test (ILD) between ITS and the chloroplast regions was carried out as a partition homogeneity test with 100 replicates (where p-values < 0.05 indicate significant incongruence) in PAUP v 4.0a163 (Swofford, 2002). No significant incongruence was observed through visual assessment and all ILD tests returned a p value greater than 0.05 so all further analyses were carried out on the combined dataset.

Maximum Parsimony analyses were carried out using PAUP v 4.0a163 (Swofford, 2002) on unweighted and unordered characters. Alignment gaps were treated as missing data. A heuristic search was carried out using stepwise random addition of 10,000 replicates, with TBR and Multrees on. Statistical branch support was obtained from 10,000 heuristic bootstrap replicates each starting with a random addition tree, optimised with TBR on and Multrees off.

The data were subsequently divided into seven partitions (ITS spacers, 5.8S gene, *psbA-trnH*, *rpl*32-*trn*L, *trn*L-F, *matK* coding region, *matK* intron region), and analysed under the best-fit model of nucleotide evolution for each genic region selected using the AIC criterion as implemented in MrModeltest v 2.4 (Nylander, 2004) (GTR+G for ITS spacers, *trn*L-F, *psbA-trnH* and *matK* intron region, GTR+I+G for *rpl*32-*trn*L and *matK* coding region and SYM+I for the ITS 5.8S gene). Bayesian inference (BI) phylogenetic analyses were carried out using Mr Bayes v 3.2.6 (Ronquist et al., 2012) on the partitioned dataset. Two runs with four chains each were implemented, run for 10,000,000 generations with a tree sampled every 1000th generation. The first 10% of sampled trees were discarded as burn-in and the remainder summarised as a maximum clade credibility tree and posterior probabilities (PP) extracted. For the Bayesian analyses, tree topology and node support were examined in FigTree v. 1.4.3 (Rambaut, 2007).

3.2.4 Character optimisation

For the character optimisation, a second Bayesian phylogenetic analysis was run with the samples reduced to one representative per species except for those that have multi-island distributions and were not monophyletic, such as *C. pendula.* In these cases, we included one representative from each area. Ancestral character states were then reconstructed using parsimony implemented in Mesquite v. 3.6.1 (Maddison & Maddison, 2019). Ancestral character reconstructions were mapped on the majority rule consensus tree obtained from the second-stage Bayesian analysis.

Ancestral states of eight morphological characters that have either been used traditionally to define infrageneric taxa in *Cyrtandra*, or were considered *a priori* to have potential congruence with the molecular phylogenetic tree, were analysed. Scoring of the morphological characters was carried out using living, herbarium and spirit collections at E and literature. The character matrix can be found in Appendix 3.2. Details of the character states for each character are given below followed by more detailed discussion on the character selection.

1. **Fusion of inflorescence bracts**: 0. Bracts free and not overlapping. 1. Bracts connate for some or all of their length. 2. Bracts free but overlapping, often forming a type of involucre. **Fig. 3.1**

   Three character states were identified for this character. There is a clear distinction at the extremes of this character between the strongly fused, involucrate, many-flowered inflorescences of species such as *C. polyneura* from Sulawesi (character state 1) and the single or paired flowers of, for example, *C. cleopatrae* from Palawan with its narrow bracts (character state 0) . Inbetween are the species with large, ovate, often overlapping bracts which are not fused but function somewhat like an involucre in species such as *C. oblongifolia* and *C. atrichos* from Borneo (characters state 2). This character is not always clearly recorded in descriptions and can sometimes be difficult to see on older specimens but is generally a relatively easily observable feature. Bract size and fusion was used by Clarke (1883) in the delimitation of a number of his sections such as 'bracts small' in *Apertae* and 'bracts large and fused' in *Jackianae*.

2. **Leaf arrangement**: 0. Leaves opposite and subequal. 1. Leaves opposite and strongly anisophyllous. 2. Leaves appearing alternate. **Fig. 3.2**

   There is a strong tendency throughout the Gesneriaceae for the two leaves of an opposite pair to be unequal in size to some degree. For the purpose of this investigation, anisophylly was taken to include species where the smaller leaf in a pair is less than a quarter the length of the larger leaf. In general, this is an easily observable character although it is important to note that the feature, although diagnostic for some species, such as *C. elatostemoides* from Palawan, can vary within others, such as *C. luteiflora* from Sulawesi where it varies even within an individual plant. Leaf arrangement is used by Clarke (1883) as one of the key characters to define Section *Dissimiles* where leaves are 'opposite, very dissimilar, the other very small or rudimentary, linear or obsolete' or 'leaves opposite, subequal' for Section *Cuneatae*.

3. **Ovary indumentum**: 0. Glabrous. 1. With a covering of eglandular hairs. 2. With a covering of sessile glands or glandular hairs. **Fig. 3.3**

   As long as flowers are available for dissection, this is an easily observable character. Only three states were designated but there is clearly some variation within the glabrous group with a number of the

glabrous-ovary species having a distinctive flush of glandular or eglandular hairs at the junction between the very top of the ovary and the base of the style (eg *C. cupulata* and *C. wallichii*). Further subdivision of this character might prove useful in the future. Clarke (1883) mentions ovary indumentum in his description of Section *Polynesieae* where he describes the species as having 'ovary glabrous or sparsely pilose' and glabrous ovaries are a character defining Section *Aureae.*

4. **Habit**: 0. Epipyte. 1. Herb. 2. Shrub or small tree. 2. Climber (woody vine). **Fig. 3.4**

   Most species are easy to assign to these different character states for this character although there are a few that straddle the boundary between herb and shrub, being described as, for example, 'woody' or 'branching' herbs. Following Beentje (2015) herbs were considered to be plants without a persistent woody stem above ground and a shrub as a 'self-supporting woody plant branching at or near the ground or with several stems from the base'. Where the delimitation was difficult the taxa were scored in both categories. Some species, such as *C. oblongifolia* from Borneo and *C. hypogaea* from Sulawesi are recorded as growing as ground shrubs or as epiphytes. These species are also scored as having both character states. Habit was not used by Clarke (1883) to define his sections. Burtt (1978), however, in his studies of *Cyrtandra* across its distribution was struck by the lack of shrubby *Cyrtandra* in Borneo and their prevalence in the Philippines and New Guinea and anticipated that this might be taxonomically informative.

5. **Disc type**: 0. Cupular. 1. Unilateral. **Fig. 3.5**

   Two disc types are defined for this character; one, cupular, where the disc completely encloses the base of the ovary and the other unilateral, where the disc is only present on one side of the ovary. Usually the distinction is very clear but there are a few species, such as *C. keithii*, where the disc encloses the ovary but is much lower on one side than the other. These cases are scored as cupular discs. Disc type is used by Clarke (1883) in his sectional classification. Both Sections *Dispares* and *Stellatae* are described as having unilateral discs.

6. **Fruit shape**: 0. Linear. 1. Ovoid. 2. Subglobose. 3. Oblong. **Fig. 3.6**

   There is a marked difference in fruit type between dry, indehiscent capsules in the west of *Cyrtandra's* distribution and fleshy berries in the east and this appears to be a key innovation in terms of successful dispersal across the Pacific (Burtt, 2001; Johnson et al., 2017; Atkins et al., 2020). Fleshiness would be an interesting character to study in more detail as has been done in other groups such as Campanulaceae (Lagomarsino et al., 2014) and Myrtaceae (Biffin et al., 2010). It is, however, challenging to score for *Cyrtandra.* Fleshiness is lost through the drying process of making a herbarium collection and is not often recorded by collectors; it is interestingly also seldom recorded in descriptions. Schlechter (1923), for example, rarely included details of fruits in his species descriptions. Another difficulty is that the change to fleshiness may only occur at the very end of

ripening, and then only briely. Burtt (2001) noted that in cultivation at Edinburgh, fruits of *C. macrotricha* developed slowly and remained hard and green for some time before turning white and fleshy for only 2-3 days before dropping. Scored instead for this analysis is fruit shape. By far the majority of fruits in *Cyrtandra* are ovoid or oblong but there are few species with distinctive linear fruits and the fleshy berries of the Pacific region are usually sub-globose. Linear fruits are distinguished from oblong by a ratio of length to width greater than 8 to 1. Fruit shape is used by Clarke (1883) in his system, for example in his descriptions of Section *Whitia* and Section *Cuneatae*.

7. **Calyx type**: 0. Calyx in three separate parts divided completely to base. 1. Calyx tubular with five very short lobes, lobes less than 1/3 overall length of calyx. 2. Calyx with all five lobes divided to near the base. 3. Calyx with some or all five lobes divided to half way, often somewhat bilabiate. 4. Calyx spathulate, cleft to the base on one side to form one large lobe opposite a sinus. 5. Calyx with fewer than five lobes (but lobes not divided to base). 6. Calyx rupturing. **Fig 3.7**

   Calyx shape is variable in *Cyrtandra* and has been used by Clarke (1883) in his sectional descriptions with, for example, the distinctive tripartite calyx, completely divided to base, used to define Section *Dissimiles* and 'calyx deeply divided' in Section *Macrosepalae*. Defining and scoring meaningful and consistent character states has been challenging with this character. The most variable state is character state 3 which may need to be futher subdivided in future studies to distinguish between those where all of the lobes are divided to half way and those where three of the lobes are much less deeply divided than the others. Calyx persistence in fruit was also used by Clarke (1883) to define his subfamilies and by Schlechter (1923) but this can be difficult to determine as it can vary over time and is often not recorded.

8. **Corolla base colour**: 0. White. 1. Red/ pink/ purple. 2. Yellow/ Orange 4. Green. **Fig. 3.8**

   The corolla base colour, not including the colour of any markings on the corolla, is fairly consistently recorded in descriptions and on specimen labels. This character is not used by Clarke (1883) in any of his sectional descriptions and has proved to be very labile in other groups such as Campanulaceae (Lagomarsino et al., 2017). It is observed, however, to show some geographic affinity in *Cyrtandra.* Most *Cyrtandra* in both the far west and east of the distribution are white flowered (Bramley et al., 2003; Johnson et al., 2017) and other colours, including red, purple and yellow, are more prevalent in the central area including Sulawesi, the Philippines and New Guinea (Atkins et al, 2013). Colour recording can be subjective so a conservative approach has been taken here, grouping similar flower colours, such as red, pink, purple and lilac together in one group. Grouping these colours is also likely to reflect the underlying primary homology of chemistry as red, pinks and purples, for example, are the result of the presence of anthocyanins (Hilgenhof, 2019) and yellow or orange the result of the presence of carotenoids (Gao et al., 2015).

One additional, non-morphological, character, area of distribution, was recorded. High levels of endemism are reported for *Cyrtandra* with most species being restricted to a single island, province or, even, mountain (Burtt, 2001; Atkins et al., 2013). Although more complex biogeographical analyses are the focus of another chapter, evaluation of distribution specifically in relation to infrageneric classification is considered here.

9. **Distribution**:. 0. Peninsular Malaysia. 1. Thailand. 2. Sumatra. 3. Java. 4. Borneo. 5. Philippines. 6. Sulawesi. 7. Seram. 8. New Guinea. 9. Australia. 10 (A) Pacific. 11 (B) China. 12 (C) Vietnam. 13 (D) Japan and Taiwan. **Fig. 3.9**

   Each species was assigned a distribution based on herbarium collections and taxonomic descriptions. The circumscription of areas of distribution were based on our knowledge of a combination of geological information (Hall 2002, 2012), previous biogeographical studies (Atkins et al. 2001, Hughes et al. 2015) and current knowledge of species distributions and relationships in *Cyrtandra* (Atkins & Cronk 2001, Bramley & Cronk 2003, Johnson et al. 2017, Kartonegoro et al. 2018). The following states were added for the outgroup taxa: China, Vietnam, Seram.

Fig. 3.1 Character states for Character 1: Fusion of inflorescence bracts: Three character states were differentiated: 0. Bracts free and not overlapping.1. Bracts connate for some or all of their length. 2. Bracts free but overlapping, often forming a type of involucre.

Fig. 3.2 Character states for Character 2: Leaf arrangement: Three character states were differentiated: 0. Leaves opposite and subequal. 1. Leaves opposite and strongly anisophyllous. 2. Leaves appearing alternate

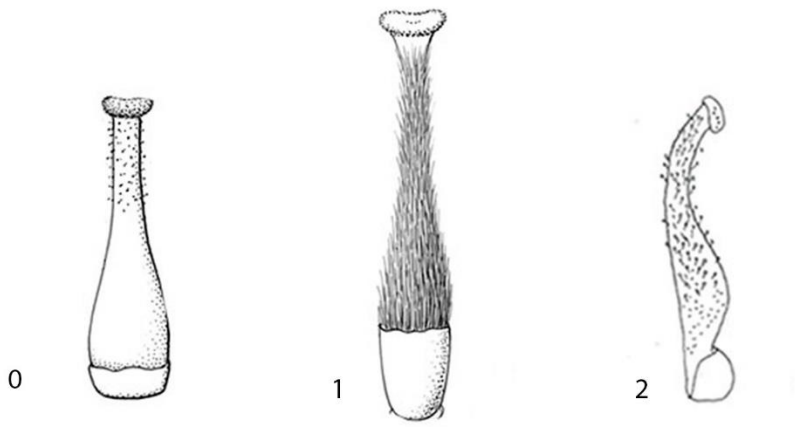

Fig. 3.3 Character states for Character 3. Ovary indumentum. Three character states were differentiated: 0. Glabrous. 1. With a covering of eglandular hairs. 2. With a covering of sessile glands or glandular hairs.

Fig. 3.4 Character states for Character 4: Habit. Four character states were differentiated: 0. Epiphyte. 1. Herb. 2. Shrub or small tree. 3. Climber (woody fine). States 0 and 3 not shown.

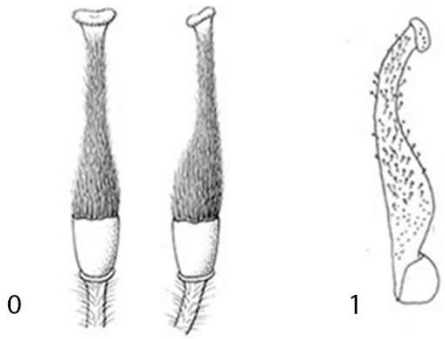

Fig. 3.5 Character states for Character 5: Disc type. Two character states were differentiated: 0. Cupular. 1. Unilateral.

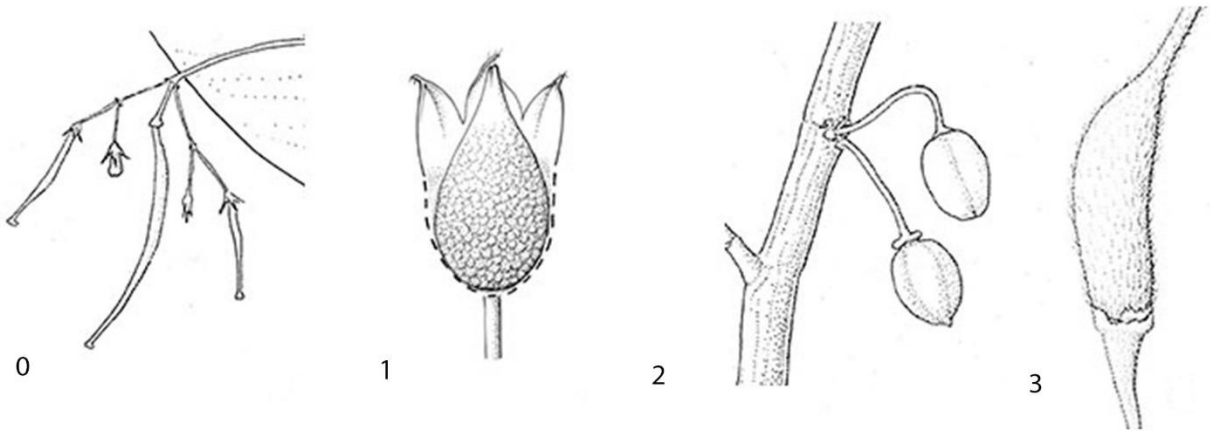

Fig. 3.6 Character states for Character 6: Fruit shape. Four character states were differentiated: 0. Linear. 1. Ovoid. 2. Subglobose. 3. Oblong**.**

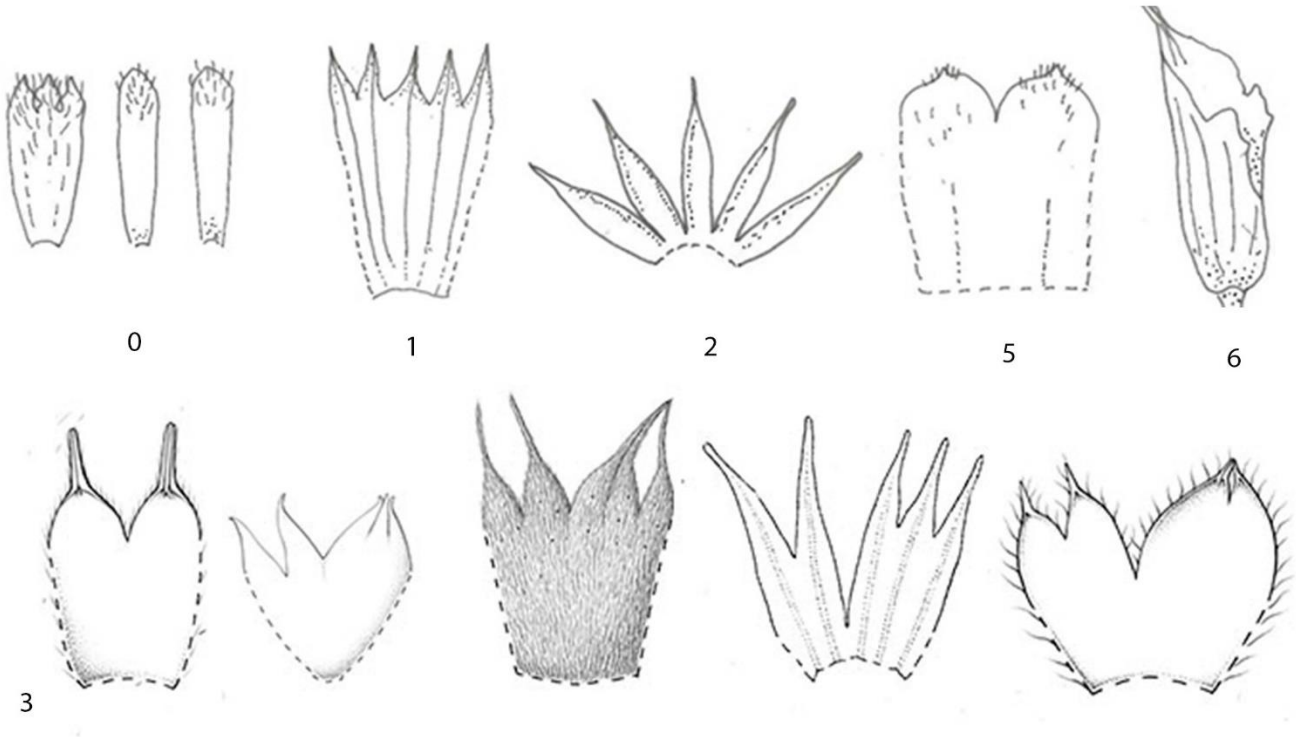

Fig. 3.7 Character states for Character 7: Six character states were differentiated. 0. Calyx in three parts.
1. Calyx tubular with very short lobes ie lobes less than 1/3 overall length of calyx. 2. Calyx with all lobes divided to base.
3. Calyx with some or all lobes divided to half way, often somewhat bilabiate.
4. Calyx spathulate, cleft to the base on one side to form one large lobe opposite a sinus. 5. Calyx with fewer than five lobes.
6. Calyx rupturing.

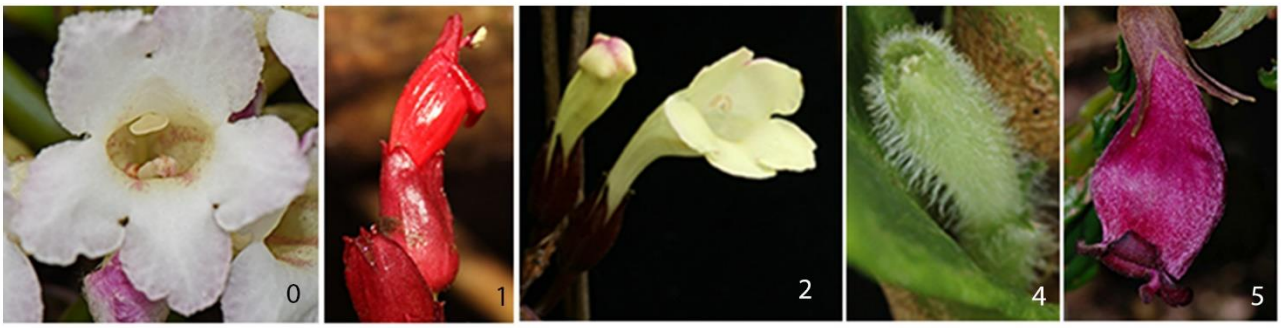

Fig. 3.8 Character states for Character 8: Corolla base colour. Six character states were differentiated. 0. White. 1. Red or pink.
2. Yellow. 3. Orange. 4. Green. 5. Purple. State 3 not shown.

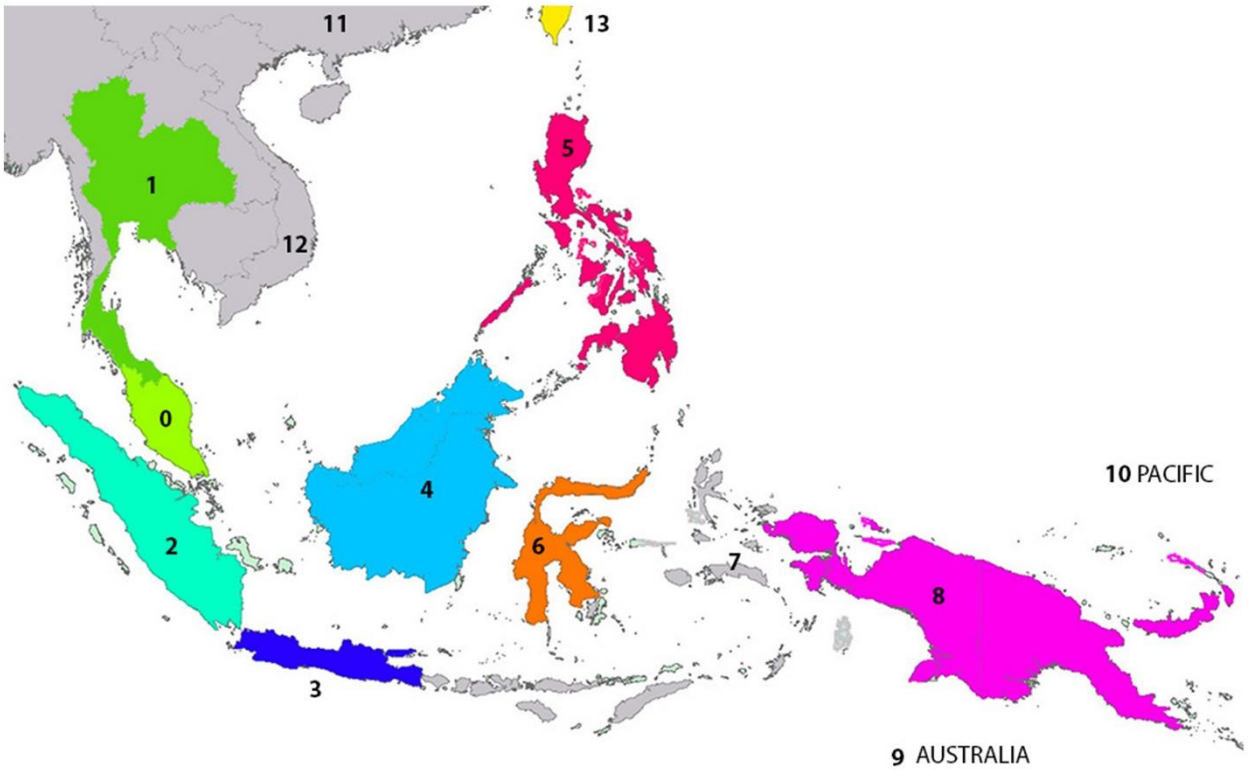

Fig. 3.9 Character states for Character 9: Distribution. Thirteen character states were differentiated. 0. Peninsular Malaysia. 1. Thailand. 2. Sumatra. 3. Java. 4. Borneo. 5. Philippines. 6. Sulawesi. 7. Seram. 8. New Guinea. 9. Australia. 10 Pacific 11 China. 12 Vietnam. 13 Japan and Taiwan.

3.2.5 Undertaking phylogenetically informed revisions of an area

Borneo and Sulawesi were selected as case studies for the phylogenetically informed revisions of a geographic area. Following Clark et al. (2013), the first step involved identifying the lineages present on those islands. Each of those lineages was then defined morphologically, primarily using the eight morphological characters used in the character optimisation exercise, but supplemented with additional characters when they were known. This information was then used to provide descriptions of these morphologically defined, monophyletic groups and to produce a key to the groups. The final step involved placing species that had not been sampled in the phylogeny within the system based on their morphology. For Sulawesi, an attempt was made to place all of the 40 known taxa and for Borneo, we placed 46 species in addition to the 26 included in the phylogenetic analysis.

3.3 Results

In total, 940 sequences were generated and our final data matrix contained five genomic regions and 5438 aligned base positions. Tree topologies of independent MP analyses of the ITS, *trn*L-f, *psb*A-*trn*H, *rpl*32 and *mat*K regions were congruent although there was far greater resolution in the ITS dataset than in any of the others individually. There were no incongruences with greater than 80% MP bootstrap support. The MP tree based on the concatenated five-gene dataset (Fig. 3.10, 3.11) largely followed the topology of the ITS tree with increased support for the relationships amongst the major clades. ML, MP and BI analyses of the combined dataset resulted in trees with congruent topologies.

3.3.1 Phylogenetic patterns and relationships

There are six major clades in the phylogeny of *Cyrtandra* in southeast Asia, evident in both the full (Fig. 3.10 & 3.11) and reduced data sets (Fig. 3.12). Most of the major clades are well supported, with all but Clade 2 having ML and MP bootstrap support values above 86 and Bayesian support values of 1.0 (Fig. 3.10 & 3.11). The relationships amongst the clades, however, are not always resolved. The clades correspond broadly to geographic areas, with the four most basally branching clades containing primarily species from locations on the Sunda shelf (Borneo, Sumatra, Palawan, Thailand, Peninsular Malaysia, Java) with two species from Sulawesi and one from Leyte in the Philippines. The more nested clades contain species from Wallacea and further east (Sulawesi, the Phiippines, New Guinea and the Pacific) although there are a small number of Sunda shelf species that are also present. The biogeography of these clades is discussed in more detail in Chapter Four.

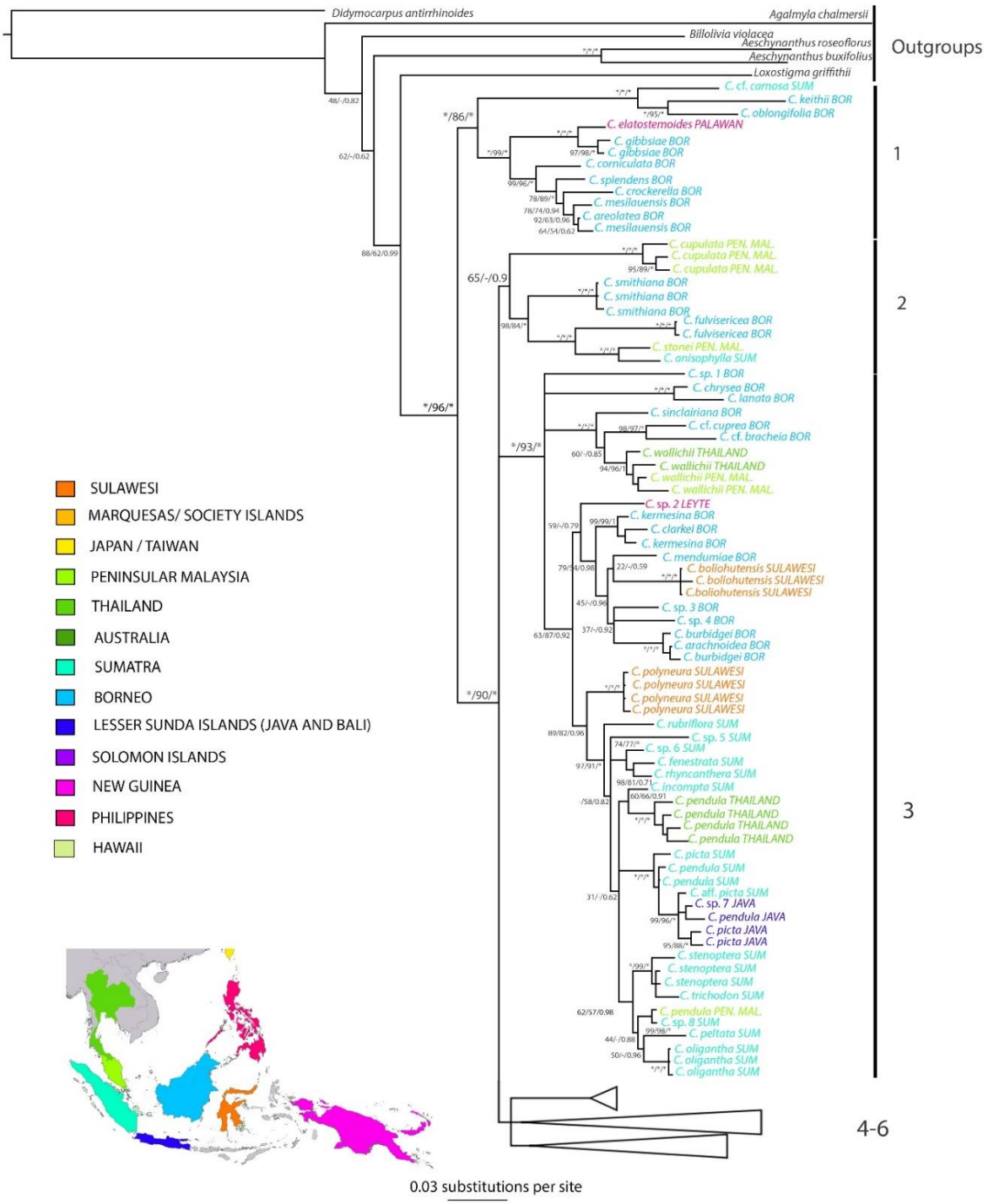

Fig. 3.10 Bayesian inference tree of *Cyrtandra* based on the combined ITS, *psb*A-*trn*H, *rpl*32-*trn*L, *trn*L-F, and *mat*K regions and highlighting the three basally branching major clades (1, 2 and 3). Node support is indicated as Maximum likelihood Bootstrap support (ML-BS), Maximum Parsimony Bootstrap support (MP-BS) and Bayesian Posterior Probabilities (BI-PP). Maximum values (100% BS or 1.0 PP) are indicated by *. No support (< 50% BS or 0.50 PP) is indicated by -. Species names are colour-coded by geographic region. Pacific islands not shown on map.

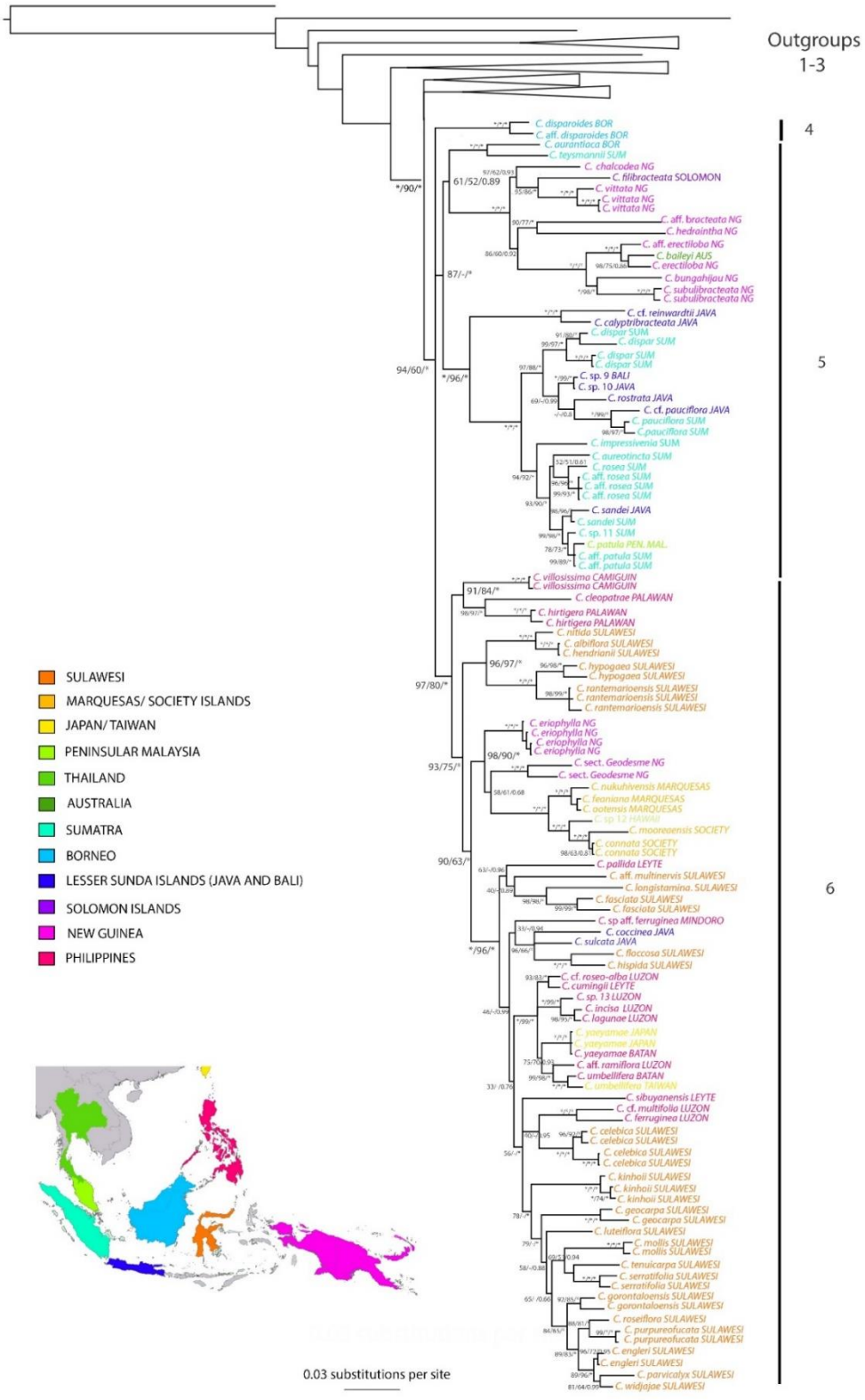

Fig. 3.11 Bayesian inference tree of *Cyrtandra* based on the combined ITS, *psb*A-*trn*H, *rpl*32-*trn*L, *trn*L-F, and *mat*K regions, and highlighting major clades 4-6. Node support is indicated as Maximum Likelihood Bootstrap Support (ML-BS), Maximum Parsimony Bootstrap Support (MP-BS) and Bayesian Posterior Probabilities (BI-PP). Maximum values (100% BS or 1.0 PP) are indicated by *. No support (< 50% BS or 0.50 PP) is ndicated by -. Species names are colour-coded by geographic region. Pacific islands not shown on map.

3.3.2 Evaluation of the existing infrageneric system in a phylogenetic context

Species sampling from across the southeast Asian region allows us to consider the monophyly and utililty of the sectional classification proposed by Clarke (1883) which is the only one that covers the full distribution of the genus and that is relevant to the large and species-rich islands of Borneo, Sulawesi and the Philippines.

Only one of the sections for which we have more than one species (eleven of Clarke's original thirteen) is resolved as monophyletic in this analysis although there are undoubtedly groups of morphologically similar species that fall together within the tree (Fig. 3.12). For Section *Aureae,* although some of the species assigned to this section, such as *C. aurantiaca* and *C. teysmannii* from Borneo and Sumatra (sub-clade L) are sister, the section is polyphyletic with species in five separate sub-clades. The two species in Section *Coccinea*, one from Java and one from Sulawesi, are not monophyletic; resolving in separate sub-clades within the same major clade (clade 6). For Section *Cuneatae,* the two species assigned to this section, *C. sandei* and *C. calyptribracteata,* are not monophyletic, occurring in separate sub-clades (N and P). Species from Section *Decurrentes* fall within four different clades although there is one sub-clade (F) containing *C. sinclairiana* from Borneo, *C. wallichii* from Thailand and Peninsular Malaysia and the two undescribed Bornean species, *C*. cf. *bracheia* and *C*. cf. *cuprea*, which can all be assigned to this section. Also within this section, *C. fenestrata* and *C. rhyncanthera* resolve as sister species in a separate clade (sub-clade J).

For *Dispares*, two of the species in this section, *C. dispar* from Sumatra and *C. rostrata* from Java, are in the same sub-clade (O) but some distance from the morphologically similar *C. disparoides* from Borneo (sub-clade K). Three of the four species assigned to section *Dissimiles* are in a strongly supported clade (sub-clade D). They are from Borneo, Peninsular Malaysia and Sumatra. A fourth species, *C. incisa*, from the Philippines assigned by Clarke to this section (1883) but not showing the key features of this section (Bramley, 2003) falls in a distantly related clade (sub-clade V). If only the three species correctly assigned to this section are considered, section *Dissimiles,* is monophyletic based on this sampling. All of the species assigned to section *Jackianae* resolve within a single clade (sub-clade J) but with two species from Section *Aureae.* Three of the four species assigned to section *Polynesieae*, all from the Society Islands and the Marquesas, are in one clade with a species from section *Macrosepalae* (sub-clade S). The other species is in a separate clade (sub-clade M). Section *Stellatae* is highly polyphyletic with species in four different clades although two of the species, *C. chrysea* and *C. lanata* from Borneo (sub-clade E), are sister species and have subsequently been identified by Hilliard & Burtt (2004c) as being part of a group of allied species from Borneo. Two of the three species assigned to section *Whitia* fall within sub-clade A but some distance from one of its other members *C. splendens* which is in sub-clade C.

3.3.3 Character optimisation

All eight of the macromorphological characters analysed showed some degree of homoplasy across the tree (summarised on Fig. 3.13). With the exception of Clade 4, which contains two morphologically similar samples, it was generally not possible to identify character traits, or combinations of traits, which defined the six major clades. The exception to this was white corolla colour which was recorded for all species in Clades 1 and 4). There was, however, enough phylogenetic signal in most of the characters to allow the identification of synapomorphies for a few of the smaller clades. CI and RI statistics, which measure the amount of homoplasy in each character and how much of that is retained as synapomorphy on the tree respectively, are given for each of the characters in Appendix 3.4. The highest RI was recovered for Distribution at 0.72 and the lowest for Corolla colour at 0.23. Individual trees showing the evolution of each character are given in Appendix 3.3.

Character One: Fusion of bracts.

The most common character state for inflorescence bracts in *Cyrtandra* is having bracts that are free and not overlapping. This is resolved to be the ancestral state for the genus and fusion of the inflorescence bracts has evolved several times. There are three clades where all of the included species have connate bracts, such as sub-clade F containing *C. sinclariana, C. wallichii, C.* cf *cuprea* and *C.* cf *bracheia* and sub-clade N containing *C. reinwardtii* and *C. calyptribracteata.* There are three pairs of sister taxa which share the character of large, overlapping bracts that are not fused at the base such as *C. teysmannii* from Sumatra and *C. aurantiaca* from Borneo and *C. stenoptera* and *C. trichodon* from Sumatra. The majority of species, however, have small, free bracts and there are many groups of related species which share this character such as all of the species in sub-clades B, C, E, K, M, O, Q, W, X and Y. The character has a relatively high RI (0.55) confirming that it does contain useful grouping information.

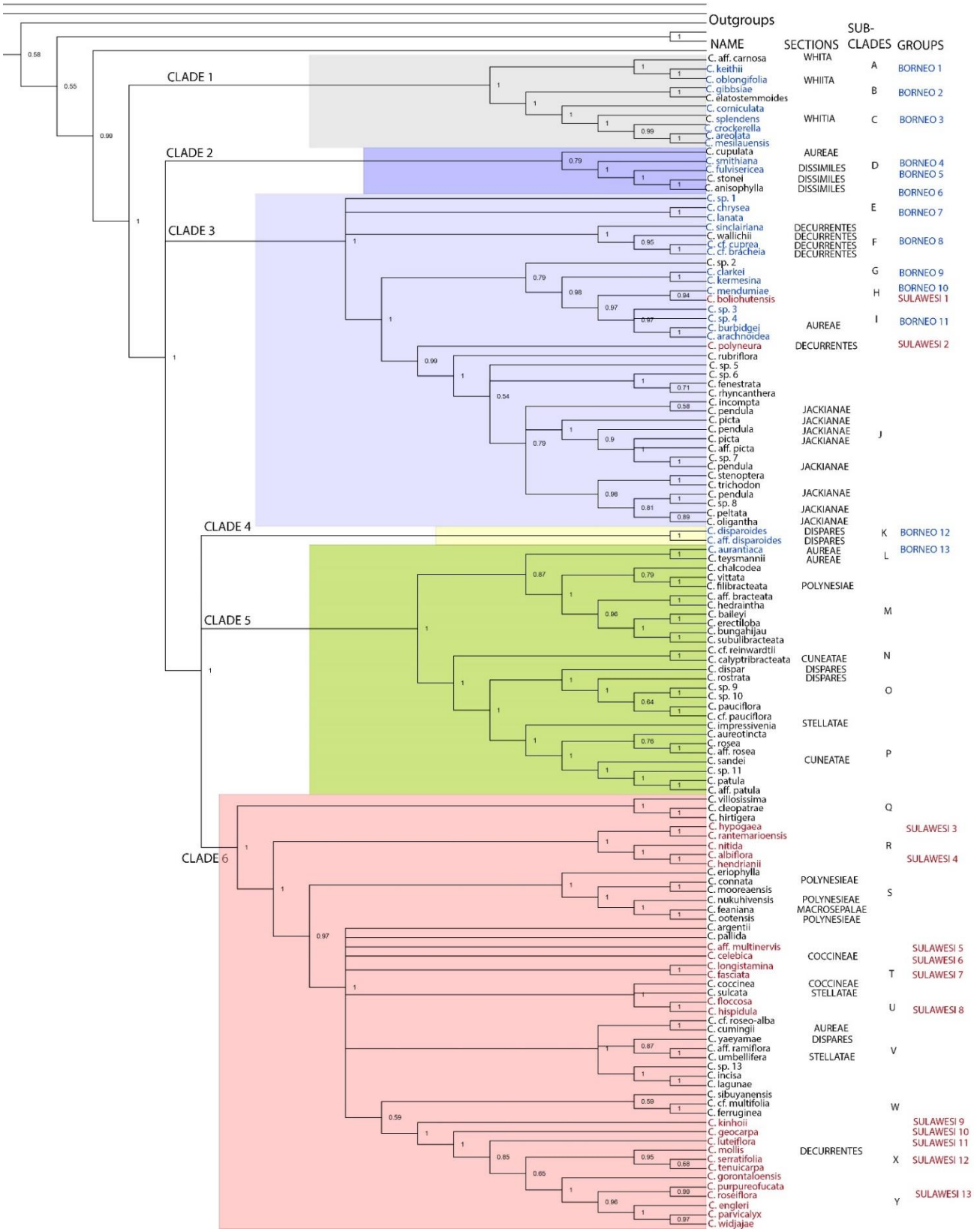

Fig. 3.12 Bayesian inference tree of reduced set of *Cyrtandra* based on the combined ITS, *psb*A-*trn*H, *rpl*32-*trn*L, *trn*L-F, and *mat*K regions. Node support is indicated as Bayesian Posterior Probabilities (BI-PP). The six major clades are highlighted by the coloured blocks. For those species referred to Clarke's sections, their affiliation is shown in the first column, followed by the names of the sub- clades used in the text. The species from Borneo are shown in blue and those from Sulawesi in red.

Character Two: Leaf arrangement.

The majority of species in *Cyrtandra* have opposite, subequal leaves and this is resolved as the ancestral state for the genus. Extreme anisophylly where one leaf of a pair is highly reduced, or where the leaves appear to be alternate and only a leaf scar is present, has evolved several times. There are four sub-clades where all of the species within the clade are either anisophyllous or appearing alternate such as sub-clade B containing *C. gibbsiae* and *C. elatostemoides* and sub-clade Y from Sulawesi. This character has an RI of 0.48.

Character Three: Ovary indumentum

The majority of species in the genus have glabrous ovaries and this is recovered as the ancestral state. An indumentum of eglandular hairs has evolved several times and there are two large clades (the *C. dispar* group in sub-clade O and the *C. engleri* group in sub-clade Y) where all of the species for which we have information have eglandular hairy ovaries. Glandular indumentum on the ovary is much less frequently observed and is diagnostic for some sub-clades, found, for example, in all species in sub-clade E from Borneo containing *C. chrysea* and *C. lanata* and sub-clade X from Sulawesi containing *C. mollis, C. serratifolia* and *C. tenuicarpa*. This character has the second highest score for RI for a morphological character in the analysis (0.58).

Character Four: Habit

Overall, the shrubby habit is the most common form for *Cyrtandra* and it is resolved as the ancestral state for clades 4, 5 and 6 and all of the subclades within. For Clade 3, however, the herbaceous form is more common with 27 of the 36 species recorded as being herbs. The epiphytic habit is observed in two sub-clades, in all species in sub-clade A and in one species, *C. hypogaea,* from Sulawesi (sub-clade R) and there is only one species in this dataset which is scored as a climber, *C. sibuyanensis* from the Philippines in sub-clade W. The ancestral state for the genus is unclear. This character has the highest RI (0.6) for a morphological character.

Character Five: Disc type

A cupular disc is the most common form of nectary disc in *Cyrtandra* and is resolved as ancestral for the genus. A unilateral disc, where the disc is only present on one side of the ovary, has evolved several times and is diagnostic for two sub-clades, including sub-clade E containing *C. chrysea* and *C. lanata* from Borneo, and and is common in the *C. dispar* clade (sub-clade O). The character has an RI of 0.47.

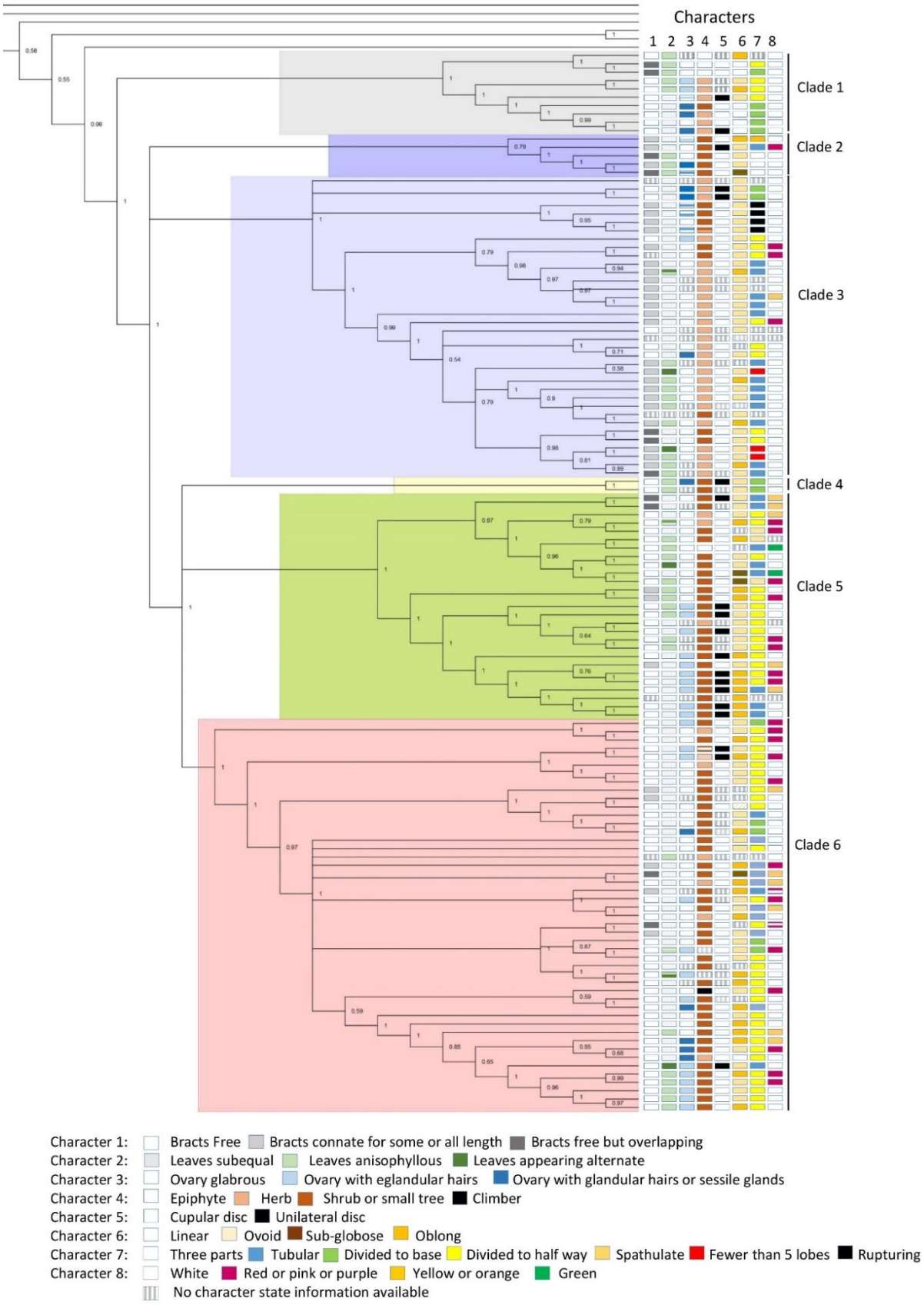

Fig. 3.13 Bayesian inference tree of reduced set of *Cyrtandra* based on the combined ITS, *psb*A-*trn*H, *rpl*32-*trn*L, *trn*L-F, and *mat*K regions. Node support is indicated as Bayesian Posterior Probabilities (BI-PP). The six major clades are highlighted by the coloured blocks. The distribution of the character states for the 8 morphological characters are shown.

Character Six: Fruit shape

The majority of species in *Cyrtandra* have ovoid or oblong fruits. The distinctive linear fruits occur in two clades in Borneo and in one species in Sulawesi and subglobose fruits have evolved in three different lineages, once in Sulawesi (sub-clade T), once in Sumatra (sub-clade D) and once in New Guinea (sub-clade M). The ancestral state for the genus is unclear and may be ovoid or linear. The character has a relatively low RI of 0.33.

Character Seven: Calyx type

The most common form of the calyx in the genus is with the lobes divided to approximately half way and this is resolved as the ancestral state for the genus and for three of the major clades. There are two calyx types which have evolved only once; the tripartite calyx, found in three species in sub-clade D and the calyx which ruptures irregularly, which is diagnostic for sub-clade F. Calyx type seems slightly more variable in the early diverging clades with five types present in major clade 3 and only three types present in clade 6, with most species having the calyx dividedd to half way. This character has an RI of 0.46.

Character Eight: Corolla colour

The majority of species in *Cyrtandra* have white corollas and this is resolved as the ancestral state for the genus. It is found in all species in Clades 1 and 4 and most species in Clades 2 and 3. Corolla colour is much more variable in Clades 5 and 6 with orange, green, yellow, red or pink and purple corollas recorded. Red or pink is the second most common flower colour after white, occurring in 25 species, somewhat scattered across the tree in species from Borneo, the Philippines, Sumatra, Sulawesi and the Solomon Islands (Clades 2, 3, 5 & 6). The least common corolla colour is green, occurring in just two species from New Guinea in Clade 5. There are a small number of clades where all of the species share the same corolla colour such as sub-clade X from the Philippines where all of the species have red or purple flowers but overall this character has little grouping information overall having the lowest RI (0.23) of all the characters assessed.

Character Nine: Distribution

The ancestral area for the genus is resolved as Borneo, congruent with the results from a recent biogeographic study of the genus in southeast Asia (Atkins et al., 2020). There is geographic structure in this dataset reflected in this character having the highest RI (0.73) of all of the characters assessed. There are ten sub-clades where all of the samples within them are from one area such as sub-clade C containing only species from Borneo, sub-clade Y with only species from Sulawesi and sub-clade Q with only species from the Philippine island of Palawan. Fifteen of the sub-clades,

however, contain species from a number of different locations, although these are usually neighbouring islands or areas. Sub-clade D, for example, contains species from Thailand, Peninsular Malaysia, Java and Sumatra and sub-clade M contains species from New Guinea, Australia and the Solomon Islands.

3.3.4 Testing of Clark et al (2013)'s concept of a phylogenetically informed revision of a geographic area

3.3.4.1 Borneo

Borneo is resolved as the most likely ancestral area for the genus (Atkins et al., 2020) and is an island of high species numbers (Atkins et al., 2013) and great morphological diversity (Burtt, 2001) for *Cyrtandra*. Twenty-four species from Borneo were included in Clarke's original system across eight sections (Clarke, 1883). Subsequently both Kraenzlin and Hilliard & Burtt have worked extensively on the island, each describing a new section (Kraenzlin, 1927; Hillliard & Burtt, 2006) and many new species (Kraenzlin, 1927; Burtt, 1978; Burtt, 1990; Burtt, 1992; Burtt, 1999; Hilliard et al., 2003; Hilliard & Burtt, 2004a; Hilliard, 2004; Hilliard & Burtt, 2005; Hilliard & Burtt, 2006) bringing the total to the island to nearly 200. There is, however, no overall synthesis of information and no key to species. Burtt (1978) described Bornean *Cyrtandra* as 'a vast sea with far too few fixed reference points'. Herbaria around the world are full of specimens from Borneo named only as *Cyrtandra* as the task of finding the correct species' name amongst the 200 available without a key is challenging (Atkins, pers. obs.).

Twenty six species from Borneo were included in this study, representing 13% of Bornean taxa. They are found in four of the major clades (Clades 1-4) and across eleven sub-clades. We were able to identify thirteen distinct lineages or groups in Borneo (Fig. 3.12), each of which could be circumscribed morphologically. All of the species in Group 7 for example are herbs with small, white corollas, calyces divided to the base and unilateral discs and all of those in Group 8 have large, connate inflorescence bracts,tubuar calyces and glabrous ovaries. Group 6 comprised a single species and two other groups comprised a single Bornean species in a sub-clade with morphologically similar species from other islands, such as *C. fulvisericea* in sub-clade D with two other species typical of Section Dissimiles from Sumatra and Peninsular Malaysia.

Most of the groups of morphologically similar species identified so far by Hilliard & Burtt in their studies of Bornean *Cyrtandra* (Burtt, 1990; Hilliard & Burtt, 2004a,b,c; 2005), were included in this study and found to be monophyletic (eg species allied to *C. chrysea* (Hilliard & Burtt, 2004c) in Group 7 and those allied to *C. fulvisericea* in Group 5). For each group we were able, following Clark et al.

(2013), to identify additional species that could be assigned to these groups based on morphology alone. We did not attempt to place all 200 species but were able to accommodate a further 46 species based on morphology alone. We have provided descriptions for each of the groups and a key. Although the sampling for Borneo is far from complete, these preliminary results suggest that a combination of geography, morphology and phylogeny provides an initial framework to allow us to start to tackle *Cyrtandra* in Borneo and to improve our ability to name unidentified specimens. The real test will come when we sequence additional collections or are faced with specimens that we are unable to place in any of the morphologically defined groups.

Key to the groups of Bornean *Cyrtandra*

A key to the groups present in Borneo, a morphological description of each of the clades and a list of additional species to be assigned to each lineage is provided below. One lineage (group 6) comprised of a single, undetermined specimen was not included in the key as the material is currently insufficient for this. No species from the recently circumscribed Section *Pleuroschisma* (Hilliard et al., 2003) were available for sequencing but its key characters are so distinctive that it has been added to the key as Group 14 on the assumption that this represents an unsampled monophyletic group.

1a Leaves strongly anisophyllous (smaller leaf in pair less than ¼ length of larger leaf) 2

1b Leaves subequal 6

2a Calyx not in three separate parts 3

2b Calyx in three separate parts ..... Group 5

3a Fruits with a median septicidal split on each side and inrolled margins ..... Group 14

3b Fruits lacking a median septicidal split on each side and inrolled margins 4

4a Fruits oblong to linear; leaves subentire; large shrubs, sometimes epiphytic ..... Group 1

4b Fruits ovoid; leaves not subentire; creeping herbs or small shrubs, not epiphytic 5

5a Shrubs; inflorescence bracts with serrate margins; calyx divided to base ..... Group 12

5b Creeping or rhizomatous herbs; inflorescence bracts with entire margins; some or all calyx lobes divided to half way ..... Group 2

6a Inflorescence bracts connate for at least some of their length 7

6b Inflorescence bracts not connate 11

7a Leaves wide ovate with a distinctive membrane between the leaf bases ..... Group 4

7b Leaves various shapes and lacking a distinctive membrane between the leaf bases 8

8a Corolla red; shrubs; few-flowered inflorescences ..... Group 9

8b Corolla white; herbs; many-flowered inflorescences 9

9a Calyx rupturing to allow corolla to come through (usually somewhat tubular prior to rupturing) ..... Group 8

9b Calyx tubular with short triangular lobes, not rupturing 10

10a Flowering at base of stem below leaves; bracts often connate but not forming an involucre; calyx often strongly ridged ..... Group 10

10b Flowering in leaf axils; bracts connate and forming an involucre; calyx not strongly ridged ..... Group 11

11a Corolla orange; calyx tubular ..... Group 13

11b Corolla white; calyx not tubular, most often with all lobes divided to base 12

12a Fruits linear (usually over 20 mm long); corollas large, over 20 mm long; disc cupular ..... Group 3

12b Fruits ellipsoid (9—18 mm long); corollas small, less than 20 mm long; disc unilateral ..... Group 7

Description of groups present in Borneo. Figs. 3.14 & 3.15

Group 1.

Description: Epiphytes or shrubs with anisophyllous leaves; leathery, narrow elliptic or oblong leaves with obscure tertiary venation and subentire margin; large, ovate bracts but no bracteoles; white flowers; glabrous ovaries; unilateral discs; oblong or linear fruits.

List of species (sampled species in bold): ***C. oblongifolia*, *C. keithii***, *C. thamnodes, C. horizontalis*

Distribution: Borneo and Sumatra

Group 2.

Description: Rhizomatous or creeping herbs; anisophyllous leaves; distinctive vermiform sclereids in the leaves visible with a hand lens; small, free bracts; calyces divided to roughly half way; large, white, hairy flowers; oblong or narrow ovoid fruits with persistent calyces.

List of species (sampled species in bold): ***C. gibbsiae*, *C. elatostemmoides,*** *C. quinquenotata, C. gillettiana*

Distribution: Borneo and Palawan, Philippines

Group 3.

Description: Woody herbs and weak shrubs; elliptic subequal leaves, often mammillate, drying dark brown with serrulate leaf margins; subsessile, axillary inflorescences with inconspicous linear bracts; medium to large white, funnelform corollas; calyces very short and lobes divided to base, hairy; ovaries glabrous or with subsessile glands; narrow ovoid to linear fruits with persistent calyces

List of species (sampled species in bold): ***C. splendens*, *C. corniculata*, *C. crockerella*, *C. areolata*, *C. mesilauensi,*** *C. didissandriformis, C. dulitiana*

Distribution: Borneo

Group 4

Description: Herbs with wide ovate leaves and a conspicuous membrane between the leaf bases; red flowers; unilateral ovary discs.

List of species (sampled species in bold): ***C. smithiana*** Very distinctive species, no obvious allies

Distribution: Borneo

Group 1 - *C. keithii*
http://data.rbge.org.uk/herb/E00394432

Group 2 - *C. gibbsiae*
http://data.rbge.org.uk/herb/E00069785

Group 3 - *C. crockerella*
http://data.rbge.org.uk/herb/E00639904

Group 4 - *C. smithiana*
http://data.rbge.org.uk/herb/E00062471

Group 5 - *C. fulvisericea*
http://data.rbge.org.uk/herb/E00069809

Group 7 - *C. lanata*
http://data.rbge.org.uk/herb/E00069784

Group 8 - *C. cuprea*
http://data.rbge.org.uk/herb/E00482778

Group 9 - *C. kermesina*
http://data.rbge.org.uk/herb/E00069815

Group 10 - *C. mendumiae*
http://data.rbge.org.uk/herb/E00114021

Fig. 3.14 Plate showing representative specimens of Bornean Groups 1-10

Group 5

Description: Shrubs with anisophyllous leaves; tripartite calyces; small (less than 20mm long flowers) with glabrous ovaries and glandular styles; cupular discs.

Ref: Section Dissimiles (Bramley, 2005)

List of species (sampled species in bold): ***C. fulvisericea*****,** *C. trisepala, C. iliasii, C. bryophila, C. multibracteata, C. producta, C. impar, C. rubropicta, C. weberi.*

Distribution: Borneo, Sumatra, Peninsular Malaysia

Group 6.

Description: Herbs with subequal, mammillate leaves and white flowers.

*This clade has not been included in the key as there is currently not enough morphological information

List of species (sampled species in bold**): *C.* sp. – Bramley et al. SAN 14207**

Group 7.

Description: Herbs with many-flowered, congested inflorescences; calyces divided almost to the base, corollas small (less than 20 mm long), white variously marked with pinkish- to reddish-purple, discs unilateral, ovaries narrowed at base, styles pubescent, fruits small, ovoid (9-18 mm long).

Species formerly identified as a morphological group: species allied to *C. chrysea* and *C. eximia* (Hilliard & Burtt, 2004c) & species allied to *C. phoenicolasia* (Hilliard & Burtt, 2004b).

List of species (sampled species in bold): ***C. chrysea*****, *C. lanata*****,** *C. eximia, C. decipiens, C. dasymallos, C. nibongensis, C. villifructus, C. kostermansii, C. hottae, C. megaphylla, C. brevisetosa, C. latibracteata, C. phoenicoides, C. dorytricha*

Group 11 - *C. burbidgei*
http://data.rbge.org.uk/herb/E00069799

Group 12 - *C. disparoides*
http://data.rbge.org.uk/herb/E00062570

Group 13 - *C. aurantiaca*
http://data.rbge.org.uk/herb/E00069827

Group 14 - *C. sarawakensis*
http://data.rbge.org.uk/herb/E00259931

All specimen images downloaded from RBGE Herbarium catalogue
https://data.rbge.org.uk/search/herbarium/

Fig. 3.15 Plate showing representative specimens of Bornean Groups 1-14

Group 8

Description: Subequal, elliptic to oblanceolate leaves with toothed leaf margins; axillary, 4 to many-flowered, bracteate inflorescences; large bracts united, for all of some of their length, to from an involucre; calyces often only divided very briefly at apex, tightly enclosing corolla in bud and rupturing as corolla expands; large, white, silky hairy flowers (often over 30 mm long); glabrous ovaries often with a distinctive tuft of hairs at the apex and a glandular style; fruits ovoid, glabrous, sometimes warty, calyx not persistent.

List of species (sampled species in bold): ***C. sinclairiana, C. cuprea, C. bracheia*****,** *C. erectipila, C. subgrandis, C. multicaulis, C. woodsii, C. vulpina, C. argentata*

Distribution: Borneo, Peninsular Malaysia and Thailand

Group 9

Description: Shrubs with subequal leaves; bright red, silky hairy, large corollas; glabrous ovaries and glandular styles; ovoid, verrucose fruits without persistent calyces.
List of species (sampled species in bold): ***C. kermesina*, *C. clarkei,*** possibly also *C. adnata* although flowers white.
Distribution: Borneo

Group 10.

Description: Herbs; inflorescences with bracts which are briefly connate at the base and often flowering at the base of the stem below the leaves; tubular, highly ridged calyces with short, triangular lobes; large, funnelform white silky hairy flowers with some markings; glabrous ovaries and cupular discs.
List of species (sampled species in bold): ***C. mendumiae,*** *C. basiflora, C. tenebrosa, C. sandakanensis* (***C. boliohutensis*** from Sulawesi)

Distribution: Borneo and Sulawesi

Group 11

Description: Herbs with subequal leaves; axillary inflorescences with connate, involucrate bracts; white to pale yellow flowers often with markings; tubular calyces.
List of species (sampled species in bold): ***C. burbidgei, C. arachnoidea****, C. neiothantha, C. warburgiana, C. ochroleuca, C. robusta, C. megalocrater*

Distribution: Borneo

Group 12 .

Description: Shrubs with strongly anisophyllous, oblanceolate leaves; inflorescences with large, serrate, free bracts; flowers white, often with two yellow guidemarks and long lower lip.
List of species (sampled species in bold): ***C. disparoides****, C. uniflora, C. athrocarpa, C. cerea, C. serratobracteata, C. libauensis*

Distribution: Borneo

Group 13.

Description: Shrubs with opposite, subequal leaves; inflorescences with free but overlapping bracts; flowers with tubular calyces, glabrous ovaries with unilateral discs.

List of species (sampled species in bold): ***C. aurantiaca, C. teysmannii*** from Sumatra

Distribution: Borneo and Sumatra

Group 14.

Description:

Herbs with anisophyllous leaves; free bracts, calyces divided almost to the base; corollas white; ovaries glabrous but crowned with a coma of long hairs; discs cupular; fruits oblong with a median septicidal split on each side and inrolled margins

Species formerly identified as a morphological group: Section *Pleuroschisma* Hilliard et al. (2003).

List of species (sampled species in bold): *C. linauana, C. coacta, C. angustielliptica, C. insolita, C. tesselata, C. penduliflora, C. sarawakensis, C. hoseana, C. tunohica, C. seganica*

Distribution: Borneo

3.3.4.2 Sulawesi

The *Cyrtandra* of Sulawesi are well known taxonomically and currently comprise 40 species (Chapter Two). Five species were included in Clarke's original classification and placed in four different sections (Clarke, 1883). Subsequently, newly described species have not been placed in sections (Atkins, 2004; Bone & Atkins, 2013; Kartonegoro et al., 2018). Twenty seven species were included in this analysis respresenting 68% of known species. Two of the species, *C. sandei* and *C. sulcata* were represented by samples from Java but the species are also present in Sulawesi. They are found in three of the major clades (Clades 3, 5 and 6) with the vast majority (24 of the 27) in Clade 6 with species from the Philippines, Taiwan, Japan, New Guinea and the Pacific. Due to the relative lack of resolution in Clade 6, several groups needed to be recognised, with five of the groups initially comprising a single species. It was possible to identify morphological characters which defined each of these groups and place all but one of the remaining unsampled species in to the system. We have provided descriptions for each of the groups and a key below. Although the approach works reasonably well for Sulawesi, there were some surprising results; ie groups of species that were apparently similar morphologically but not closely related, such as *C. fasciata* and *C. kinhoii,* which are difficult to differentiate in the herbarium, but were resolved in separate clades. The morphological descriptions of these two groups (Group 8 and Group 10) were so similar that it made the placement of a fourth similar species, *C. flavomaculata,* difficult. Both of the species in Group 9, however, have distinctive glandular styles so it was decided to place *C. flavomaculata* in this group as it shares this unusual character. The morphologically very different *C. serratifolia,* a prostrate herb with small serrate leaves, ovoid fruits and large red flowers, was sister to *C. tenuicarpa,* a shrub with large, entire leaves, linear fruits and small white flowers (Group 13). They do, however, have the same calyx type, bract fusion, leaf arrangement and perhaps, most importantly, unusual glandular ovary indumentum. It will undoubtedly be a gradual process of recipricoal illumination as we learn

which morphological characters are diagnostic of monophyletic groups at different hierarchical levels in the *Cyrtandra* phylogeny.

Key to groups in Sulawesi

1a Inflorescences on long, trailing stems originating at the base of the plant 2

1b Inflorescences axillary, in current leaf axils or at base of stem, or cauliflorous 4

2a Ovary (and usually fruit) densely eglandular hairy; ovary disc unilateral ..... Group 4

2b Ovary and fruit glabrous; ovary disc cupular 3

3a Corolla white ..... Group 11

3b Corolla yellow ..... Group 12

4a Inflorescence cauliflorous ..... Group 7

4b Inflorescence axillary, in current leaf axils or at base of stem below current leaves 5

5a Inflorescence bracts fused for some or all of their length 6

5b Inflorescence bracts free for their whole length 7

6a Inflorescences in the axils of current leaves, bracts fused and forming an involucre ..... Group 2

6b Inflorescences at base of stem below current leaves; bracts fused only briefly ..... Group 1

7a Ovary (and usually fruit) hairy, either glandular or eglandular 8

7b Ovary and fruit glabrous 9

8a Ovary glandular hairy ..... Group 13

8b Ovary eglandular hairy 13

9a Calyx divided to approximately half way 10

9b Calyx tubular, divided only briefly at apex 11

10a Inflorescence bracts free, linear ..... Group 5

10b Inflorescence bracts free, large and overlapping ..... Group 6

11a Style glandular hairy 12

11b Style glabrous ..... Group 10

12a Leaves decurrent at base ..... Group 8

12b Leaves not decurrent ..... Group 9

13a Leaves opposite, subequal; calyx tubular with short lobes ..... Group 3

13b Leaves anisophyllous or appearing alternate; calyx divided to approximately half way ..... Group 14

Description of groups present in Sulawesi. Figs. 3.16-3.18

Group 1

Description: Herbs; inflorescences with bracts which are briefly connate at the base and often flowering at the base of the stem below the leaves; tubular, highly ridged calyces with short, triangular lobes; large, funnelform white silky hairy flowers with some markings; glabrous ovaries and cupular disks.

List of species (sampled species in bold): ***C. boliohutensis*** (From Borneo: ***C. mendumiae****, C. basiflora, C. tenebrosa, C. sandakanensis*

Distribution: Borneo and Sulawesi (This is the same as Borneo Group 10)

Fig. 3.16 Plate showing representative species of Sulawesi Groups 1-6

Group 2

Description: Herbs with subequal leaves with decurrent leaf-bases; inflorescences axillary with large, connate bracts forming an involucre; calyces tubular; corollas white with markings in throat; discs cupular; ovaries glabrous; fruits ovoid

List of species (sampled species in bold): ***C. polyneura****, C. hekensis, C. rubribracteata*

Distribution: Sulawesi

Group 3

Description: Herbs or shrubs with subequal leaves and decurrent leaf bases; inflorescences with free bracts; calyces tubular; ovaries densely eglandular hairy; fruits oblong.

List of species (sampled species in bold): ***C. sandei,*** *C. jellesmani*

Distribution: Sulawesi, Java and Sumatra

Group 4

Description: Shrubs with subequal leaves; inflorescences trailing from the base of the plant; inflorescence bracts free; calyces divided to approximately half way; corollas less than 20 mm long; ovaries with eglandular hairs and unilateral discs; fruits with persistent calyces.

List of species (sampled species in bold): ***C. hypogaea C. rantemarioensis***

Distribution: Sulawesi

Group 5

Description: Subequal leaves with decurrent leaf bases; subsessile, axillary inflorescences with free, linear bracts; calyces divided to approximately half way; corollas less than 15 mm long with cupular discs and glabrous ovaries; fruits ovoid.

List of species (sampled species in bold): ***C. albiflora, C. hendrianii, C. nitida, C. longirostris***

Distribution: Sulawesi

Group 6.

Description: Shrubs with subequal leaves; axillary inflorescences with large, overlapping bracts; calyces with lobes divided to approximately half way; ovaries glabrous with cupular discs.

List of species (sampled species in bold): ***C.*** **aff.** ***multinervis*****,** *C. multinervis*

Distribution: Sulawesi

Fig. 3.17 Plate showing representative species of Sulawesi Groups 7-12

Group 7

Description: Shrubs with subequal leaves**;** cauliflorous inflorescences with slightly connate bracts; calyces tubular; corollas red with cupular discs and glabrous ovaries.

List of species (sampled species in bold): ***C. celebica****, C. spicata*

Distribution: Sulawesi

Group 8

Description: Shrubs (and occasionally epiphytes) with subequal leaves; tubular calyces; corollas with strongly recurved lower lobes, glabrous ovaries, glandular styles and cupular discs.

List of species (sampled species in bold): ***C. longistamina, C. fasciata****, C. flavomaculata, C. purpurea*

Distribution: Sulawesi

Group 9.

Description: Herbs or shrubs with subequal leaves; axillary inflorescences with free bracts; yellow or white corollas and ovoid or oblong fruits.

List of species (sampled species in bold): ***C. floccosa, C. hispidula, C. sulcata***

Distribution: Sulawesi and Java

Group 10

Description: Shrubs or small trees with subequal leaves; many-flowered axillary inflorescences with large, free bracts; tubular calyces; small, white corollas with glabrous ovaries and styles and cupular discs.

List of species (sampled species in bold): ***C. kinhoii***

Distribution: Sulawesi

Group 11

Description: Herbs or shrubs with subequal leaves; inflorescences on trailing stems from the base of the plant; bracts free, linear; calyces divided to half way; corollas large, white with glabrous ovaries and cupular discs.

List of species (sampled species in bold): ***C. geocarpa***

Distribution: Sulawesi

Group 12

Description: Herbs or shrubs with subequal or anisophyllous leaves; inflorescences on long trailing stems at the base of the plant; bracts free, linear; calyces divided to approximately half way; corollas large, yellow with glabrous ovaries and cupular discs.

List of species (sampled species in bold): ***C. luteiflora***

Distribution: Sulawesi

Group 13

Description: Herbs or shrubs; inflorescences with bracts free, linear; calyces divided to approximately half way; corollas with cupular discs and glandular hairy ovaries.

List of species (sampled species in bold): ***C. mollis, C. tenuicarpa, C. serratifolia, C. bruteliana***

Distribution: Sulawesi

Group 14

Description: Shrubs mostly with anisophyllous or alternate leaves; axillary inflorescences with free, linear bracts. Calyces divided to approximately half way; corollas with densely hairy ovaries.

List of species (sampled species in bold): ***C. purpureofucata, C. gorontaloensis, C. roseiflora, C. engleri, C. parvicalyx, C. widjajae*** *C. sopuensis, C. kjellbergii, C. balgooyi, C. gambutensis,, C. spectabilis.*

Distribution: Sulawesi

Fig. 3.18 Plate showing representative species of Sulawesi Groups 13-14

3.4 Discussion

Understanding the evolutionary and taxonomic relationships in southeast Asian *Cyrtandra* and tackling its taxonomy has been complicated by a broad geographic range and high species numbers. Assessing species relationships and morphological character evolution across Southeast Asia for the first time using molecular and morphological data allows us to consider the efficacy of the current infrageneric system, the diagnostic utility of a range of characters at different hierarchical levels in the phylogeny and to evaluate possible approaches to future revisionary work:

(i) Evaluation of the genus-wide infrageneric system in a phylogenetic context

Based on current sampling, only one of Clarke's sections, *Dissimiles,* is monophyletic; the others are polyphyletic. Clarke's system has not been used consistently for some time and considered unworkable by a number of authors (Kraenzlin, 1913; Schlechter, 1923; Gillett, 1975; Burtt, 2001) with new species generally not being assigned to a section when they are published (see Burtt 2001; Atkins & Cronk 2001; Bramley et al. 2004; Johnson 2017; Kartonegoro et al., 2018). This study provides confirmation that the current classification does not reflect monophyletic groups and it is clear that a new system or approach is required for *Cyrtandra*.

(ii) Testing of a selection of key macromorphological characters to determine their degree of homoplasy and to assess their suitability for diagnosing any future infrageneric classification

All of the macromorphological characters evaluated in this study showed homoplasy. The lability of macro-morphological characters is well documented in angiosperms, especially those associated with reproductive structures (Lavin et al., 2001; Lagomarsino et al, 2014, 2017; Vasconcelos et al., 2015; Parpiorek et al., 2016; Hilgenhof, 2019) and has been previously predicted in *Cyrtandra;* the great morphological diversity in Pacific *Cyrtandra* expected to include 'a great deal of parallel evolution' (Gillett, 1973). All of the characters did however define clades individually, or in combination, in some parts of the tree. All of the species in sub-clade A, for example, are epiphytes with highly anisophyllous leaves and with white corollas. All of those in sub-clade F have calyces that rupture irregularly and large, connate inflorescence bracts. Of all of the characters tested, those that have the most grouping information are habit, ovary indumentum and fusion of bracts. Corolla colour was the least phylogenetically informative character; presumably as it is under strong pollinator driven selection.

Research on anatomical characters such as pollen (Leugmayr, 1993; Schlag-Edler & Kiehn, 2001) and foliar sclereids (Bokhari & Burtt, 1970; Burtt & Bokhari, 1973; Atkins & Cronk, 2001; Bramley, 2003) on a small subset of *Cyrtandra* have shown some taxonomic signal but there is currently not enough information available to assess them systematically across the genus although preliminary mapping

of both foliar sclereids and pollen suggests that these characters may be homoplastic when considered across a wider sample and, even, variable within some species (Atkins, 1999; Bramley, 2003; Schlag-Edler & Kiehn, 2001). Interestingly, unlike other large genera in Gesneriaceae such as *Streptocarpus* and *Aeshynanthus* (Rashid et al., 2001; Nishii et al., 2015), no variation has been observed in chromosome counts across the genus with all published counts being 2n=34 (Möller & Pullan, 2015 onwards). These counts come from 45 species of *Cyrtandra* from Peninsular Malaysia, Borneo and Hawaii, and from five of the six major clades. Burtt in his 2001 review of *Cyrtandra* suggested a number of additional characters which might be worth considering for future study including (i) the different mechanisms for protecting the terminal bud, (ii) the way in which young leaves are rolled or folded, (iii) corolla aestivation and (iv) the shape of the placentae. All of these characters would require detailed field observation or laboratory work and although additional morphological information would be useful, the scoring of anatomical, cytological or morphological characters that are difficult to see on herbarium collections, may prove prohibitively time consuming in a genus of over 800 species - and of limited utility in future herbarium identification. Discovery of additional taxonomically informative and easily observable macromorphological characters would be valuable for *Cyrtandra*. Researchers in the large herbaceous genus *Begonia*, for example, have managed to find strong corroboration between certain macro-morphological characters and major clades such as the presence of different perennation organs (Thomas et al., 2011; Moonlight et al., 2018); those in *Myrcia* with branching type and hypanthium morphology (Lucas et al., 2011; 2018); hair type in *Solanum* (Särkinen et al., 2015; 2018); and anther appendages in *Globba* (Williams et al., 2004; Sangvirotjanapat et al., 2018).

(iii) Testing of Clark et al. (2013)'s concept of a phylogenetically informed revision of a geographic area on two species-rich islands in southeast Asia:

For Borneo, with c. 200 species, and great morphological and phylogenetic diversity, it was possible to define groups and find additional species that could be placed in those groups based on morphology alone. Our knowledge of *Cyrtandra* on the island allowed us to supplement the key and descriptions with additional morphological characters. This, however, represents only the first tentative steps to tackling a revision of *Cyrtandra* on the island and we will only have a better understanding of how successful this approach is once more samples are added.

For Sulawesi where the taxonomy is well known, the species numbers are relatively low and the species cluster phylogenetically, predominantly in just one of the major clades, it was also possible to morphologically define groups and to place all of the unsampled taxa in to these groups. Again, our knowledge of the genus on the island, allowed us to supplement the eight characters with extra character information to augment the descriptions and key. The system was not perfect; two of the groups were similar morphologically based on our scoring but could be differentiated by the addition of a style indumentum character. It was possible to write a key to the lineages.

(iv) Evaluation of approaches for future revisionary work

The main findings from this study; the homoplasy of the macromorphological characters assessed and the resultant poor diagnosability of the six major clades combined with evidence of floristic exchange between islands, suggests that a single approach, either based on geography, morphology or phylogeny, will not be satisfactory for *Cyrtandra* at this stage and, as suggested by Clark et al. (2013) a method combining all three in an integrative approach will be most successful. Undertaking a series of phylogenetically informed geographic revisions represents a pragmatic approach to future taxonomic work; allowing researchers to focus on a single, geographic area with the benefits that this offers in terms of time, logistics and finances whilst also working within an explicitly phylogenetic framework. This should help to co-ordinate research and facilitate discussion (Nic Lughada et al., 2019). The two case studies undertaken showed that this was possible not only on a relatively small island where the taxonomy is well known but, crucially, also as a tool for undertaking revisionary work on a highly diverse island with a large number of species. As outlined by Clark et al. (2013) this approach uncovers the minimum number of lineages present and provides a diagnostic key for the purposes of ongoing research allowing taxonomy to move forward rather than a formal classification.

3.5 Future directions: the need for more data

Further sampling of *Cyrtandra* across its distribution is required to complete our understanding of relationships in the genus. Combining this dataset with the complementary and expanding data on Pacific *Cyrtandra* is in progress. Additionally, releasing the wealth of data held in herbarium collections potentially accessible through improvements in DNA extraction methods and sequencing approaches (Hart et al., 2016) is critical. To complement this approach, growing interest in the genus and increased collaboration in the southeast Asian region (eg Kartonegoro et al., 2018; Olivar et al., in press) will facilitate collecting in under-sampled areas such as Kalimantan, Maluku, the southern Philippines and New Guinea.

Combining the increasing knowledge of the phylogenetic relationships in this group and the evolution of morphological characters will also facilitate the study of shifts in diversification rates in the genus and its association with key features such as fleshy fruits or vertebrate pollinated flowers as has been shown in other groups (Biffin et al., 2010; Lagomarsino et al., 2014; 2016; 2017; Lu et al., 2019).

3.6 Conclusions

It is challenging to find taxonomic solutions in a diverse group of tropical plants with high species numbers and where there is evidence of ongoing speciation. This study confirms that the existing infrageneric classification is not satisfactory. It also shows that there are high levels of homoplasy in the morphological characters selected although it was possible to use morphological characters to define clades in parts of the tree. There was some geographic structure in the resultant phylogenetic tree but this was not consistent as there was evidence of floristic exchange, particularly between neighbouring islands. Phylogenetically informed taxonomic revisions of geographic areas, an approach which combines evidence from molecular, morphological and distribution data represents a practical approach for tackling species delimitation in *Cyrtandra* across its distribution. It has proved possible to identify and morphologically define clades in Borneo and Sulawesi and to provide identification keys to these groups. Although the sampling for Borneo is not complete, this approach should allow the *Cyrtandra* of that island to be tackled systematically for the first time and to improve our ability to name, or describe if new, unidentified specimens. Completing our understanding of evolution and relationships in this genus will allow us to maximise the use of *Cyrtandra* as a tool for studying biogeography, speciation, diversification and conservation prioritisation in the rainforests of Southeast Asia.

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Appendix 3.1 C.B.Clarke's Infrageneric System with Subgenera and Sections listed alphabetically based on Clarke (1883)

Subgenus name	Description	Sections included
Brachycyathus	Calyx persistent on fruit. Tube short or almost absent, wide funnel-shaped or cupshaped, not cylindrical, very few teeth longer; the lobes of the flower open.	*Apertae, Cuneate, Dispares, Macrosepalae, Stellatae, Whitia*
Macrocyathus	Calyx deciduous (except in section 7); tube cylindrical, ovoid or campanulate; the teeth often shorter than the tube length; the teeth often shorter than the tube length. Calyx in eastivation, closed, valvae or sub spathe-like; at the base just circumscised or cleft in two, gradually deciduous? In section 7, subpersistent, surrounds fruit; in *C. ciliata* strongly 5-divided.	*Aureae, Campanulaceae, Coccinea, Decurrentes, Dissimiles, Jackianae, Polynesieae*

Sectional name	Description (Translation from Latin)	Species included in analysis
Apertae	Leaves opposite, similar. Fruit shorter than calyx, teeth triangular-lanceolate, subcoriaceous, in aestivation open or stellate. Inflorescence cymose, bracts small. Ovary glabrous, or bearing glands, not villous. Disc annular.	**None – Hawaii only**
Aureae	Leaves opposite, subequal (leaves pseudo-alternate additional case), entirely petiolate (sometimes briefly); bracts large, often joined, campanulate, subpersistent. Pedicels very short, umbellate, flowers barely exserted from bracts, Corolla (except *for C. burbidgei* and *C. macrantha*) externally sericeous. Disc annular.	*C. burbidgei** *C. cumingii** *C. teysmannii** *C. cupulata* *C. trichodon* *C. aurantiaca*
Campanulaceae	Leaves opposite, petiolate. Calyx persistent longer on fruit, on the other side, split, then breaking up more (mature fruit not seen in some species). Peduncles (except in *C. baccifera*) short, many flowered or 1-flowered; bracts inconspicuous or large, not joined in an involucre; flowers pedicellate. Calyx tube longer than or equal to fruit.	**None – Fiji, Hawaii**

Coccineae	Leaves for the most part opposte (leaves pseudo alternate sometimes?), entirely petiolate. Cymes less subdense composite, many-flowered, and exserted from bracts.	*C. coccinea** *C. celebica*
Cuneatae	Leaves opposite, subequal. Calyx teeth shorter than the tube or slightly longer, ovate lanceolate-linear at base; calyx subspathulate-valvate in aestivation, before flowering sometimes mucronate or subrostrate. Peduncles short or almost absent; bracts caducous, pedicels few or many. Corolla short or medium. Fruit oblong or ellipsoid.	*C. sandei** *C. calyptribracteata*
Decurrentes	Leaves opposite, a little unequal, narrow or decurrent base. Inflorescence axillary, pedicels short, fasciculate, or peduncles short with dense sessile involucre. Calyx tubular, deciduous	*C. fenestrata** *C. rhyncanthera** *C. mollis** *C. polyneura* *C. sinclairiana* *C. wallichii*
Dispares	All leaves alternate, one of a pair abortive or reduced to a linear petiole. Bracts lanceolate, free or in *C. schizostyla* united in an involucre. Fruit ellipsoid or oblong, shorter than calyx. Corolla small or average. Disc unilateral, auriculiform or oblong.	*C. dispar** *C. rostrata** *C. yaeyamae*
Dissimiles	Leaves opposite, very dissimilar, the other very small or rudimentary linear or obsolete; in *C. fortunei* sometiems leaves subequal. Branches are often sinuous/ zigzag/ spirally twisted. Petioles usually short. Peduncles short or nearly absent; bracts soon deciduous. Flowers subsessile or pedicells fasciculate or umbellate. Calyx large, campanulate or oblong, caducous.	*C. anisophylla** *C. incisa*** *C. fulvisericea* *C. stonei*
Jackianae	Leaves opposite and pseudo alternate or all pseudo-alternate, entirely (often long) petiolate, base cordate or obtuse. Pedicels capitate or dense umbellate, sometimes solitary. Bracts large, fused, persistent or deciduous, or free, thin and small. Calyx thin, tubular-oblong with a beaked apex before flowering; lobes ovate at base. Corolla large, externally villous (except perhaps in *C. integrifolia*)	*C. oligantha** *C. peltata** *C. picta** *C. pendula**

Macrosepalae	Leaves opposite, equal or more or less equal. Calyx equal to or exceeding the fruit, deeply divided; lobes ovate, narrow or spathulate, subfoliaceous. Cymes lax sometimes few flowered. Bracts large or small, free or in joined in a subpersistent cup-like involucre. Corolla medium or small. Disc annular.	*C. feaniana*
Polynesieae	Leaves opposite, in a few 3-4-leaved, subequal, entirely petiolate. Flowers cymose, pedicels long, or in a few cases, contracted cymes, pedicels fasciculate or umbellate. Calyx often divided to half the length of the flower, lobes wide lanceolate, fine or subcoriacous, unequal, subspathulate, 2-5 lobed, deciduos at the base. Corolla externally glabrous or villose, not long seriacous, ovary glabrous or sparsely pilose. Fruit ellipsoid or in *C. dolichocarpa* linear-cylindrical.	*C. filibracteata* *C. nukuhivensis* *C. ootensis* *C. connata*
Stellatae	Leaves for the most part, opposite, equal or unequal. Calyx lobes linear or subulate-lanceolate. Peduncles short, bracts small or medium, sometimes united, involucrum for the most part not being formed, pedicels simple umbels or 1-3 cymes. Corolla small or medium, externally hairy. Disc unilateral, subquadrate. Fruits ovoid or oblong, cylindrical, not linear.	*C. chrysea** *C. sulcata** *C. impressivenia* *C. umbellifera* *C. lanata*
Whitia	Leaves of a pair often dissimilar in size. Peduncles short or nearly absent; bracts free. Calyx short, persistent; tube 0-2 mm; lobes linear. Fruit (except in *C. carnosa*) linear or linear-cylindrical.	*C. carnosa** *C. oblongifolia** *C. splendens**

***Species names marked with an asterisk were included in Clarke's original system. Others have been assigned at a later date, either by the authors of this paper or on publication of the species.**

***C. incisa* was included in Section *Dissimiles* by Clarke (1883) but does not have the morphological characters required for placement in this section (Bramley, 2003).

Appendix 3.2 Character matrix used for the Character Optimisation in Mesquite. Species are listed alphabetically.

	Bracts	Leaves	Ovary	Habit	Disc	Fruit	Calyx	Corolla	Distribution
Aeschy. buxifolius	0	0	0	0	0	0	2	1	B
Aeschy. roseoflorus	0	0	?	0	?	0	1	1	7
Ag. chalmersii	0	1	1&2	0	0	0	3	1	8
B. violacea	0	2	2	1	0	1	3	0	C
C. aff *bracteata*	0	1	0	2	0	3	4	?	8
C. aff *multifolia*	0	0	1	2	?	?	3	0&1	5
C. aff *multinervis*	?	0	?	1	?	?	?	0	6
C. aff *picta*	1	0&1	?	1	?	?	1	0	2
C. albiflora	0	0	0	2	0	1	3	0	6
C. anisophylla	2	1	0&2	2	0	2	0	0	2
C. arachnoidea	1	0	0	1	0	1	1	2	4
C. areolata	0	0	0	1	0	0	2	0	4
C. argentii	0	0	0	2	0	1	1	0	5
C. aurantiaca	2	0	0	1&2	1	1	1	2	4
C. aureotincta	1	0	1	2	0	1	3	0	2
C. baileyi	0	1	0	2	0	0	3	0	9
C. boliohutensis	1	0&1&2	0	1	0	3	1	0	6
C. bungahijau	0	0	0	1&2	0	2	1	3	8
C. burbidgei	1	0	0	1	0	1	1	0	4
C. calyptribracteata	1	1	0	2	0	1&3	3	0&1	3
C. celebica	1	0	0	2	0	3	1	1	6
C. cf *bracheia*	1	0	0&1	1&2	0	1	6	0	4
C. cf *carnosa*	0	1	?	0	?	3	?	0	2
C. cf *cuprea*	1	0	0	1&2	0	1	6	0	4
C. cf *disparoides*	0	1	?	2	?	?	2	0	4
C. cf *patula*	0	0	1	2	1	3	1	0	2
C. cf *pauciflora*	0	0&1	?	2	?	?	3	1	3
C. cf *ramifolia*	0	0&1	0&1	?	0	1&3	2	1	5
C. cf *reinwardtii*	1	1	0	2	0	1&3	3	0	3
C. cf *rosea*	0	0	1	2	1	3	3	1	2
C. cf *roseo-alba*	0	0	0	1&2	0	?	3	0&1	5
C. chalcodea	0	0	0	1	0	1	3	2	8
C. chrysea	0	0	2	1	1	1	2	0	4
C. clarkei	1	0	0	2	0	1	3	1	4
C. cleopatrae	0	0	0	1	0	1	3	1	5
C. coccinea	1	0	?	2	?	3	1	0&1	3
C. connata	1	0	?	2	?	?	3	0	A
C. corniculata	0	0	1&2	1	1	1	3	0	4
C. crockerella	0	0	2	1	0	0	2	0	4
C. cumingii	2	0	0	1&2	0	1	1	0	5

	Bracts	Leaves	Ovary	Habit	Disc	Fruit	Calyx	Corolla	Distribution
C. cupulata	1	0	0&1	2	0	3	5	0	0
C. dispar	0	1	1	2	1	1	3	0&1	2
C. disparoides	0	1	2	2	1	1	2	0	4
C. elatostemoides	0	1	1	1	?	3	3	0	5
C. engleri	0	1	1	2	0	1	3	0	6
C. erectiloba	0	2	0	2	0	1	1	0	8&A
C. eriophylla	1	0	0	2	?	?	3	2	8
C. fasciata	0	0	0	1	0	3	1	1&2	6
C. feaniana	0	0	0	2	?	1	2	0	A
C. fenestrata	0	0	0	1	0	?	3	0	2
C. ferruginea	0	0	2	2	0	3	1	0	5
C. filibracteata	0	0	0	2	0	?	4	0&1	A
C. floccosa	0	0	0	2	0	1	1	2	6
C. fulvisericea	2	1	0	2	0	1	0	0	4
C. geocarpa	0	0	0	1&2	0	3	3	0	6
C. gibbsiae	0	1	1	1	?	1	3	0	4
C. gorontaloensis	0	2	1	2	1	1	1	0&2	6
C. hedraintha	0	1	0	0	0	?	1	0	8
C. hendrianii	0	0	0	2	0	1	3	1	6
C. hirtigera	0	0	0	1&2	0	3	3	1	5
C. hispidula	0	0	0	1	0	3	1	0	6
C. hypogaea	0	0	1	0&1	1	1	3	0	6
C. impressivenia	0	0	1	2	1	3	3	0	2
C. incisa	0	1&2	1	?	?	3	3	0	5
C. incompta	1	1&2	?	1	?	?	1	0	2
C. keithii	2	1	0	0	0	0	3	0	4
C. kermesina	?	0	0	2	0	1	4	1	4
C. kinhoii	0	0	0	2	0	1	3	0&1	6
C. lagunae	0	0	?	2	?	3	3	0	5
C. lanata	0	0	2	1	1	1	2	0	4
C. longistamina	2	0	0	1&2	0	2	1	0&2	6
C. luteiflora	0	0&1	0	2	0	3	3	2	6
C. mendumiae	1	0	0	1	0	1	1	0	4
C. mesilauensis	0	0	2	1&2	?	0	2	0	4
C. mollis	0	0	2	2	0	3	3	1&2	6
C. mooreaensis	0	0	0	2	0	?	3	0	A
C. nitida	0	0	0	1	0	1	3	0	6
C. nukuhivensis	0	0	0	2	?	1	1	0	A
C. oblongifolia	2	1	0	0	0	0	2	0	4
C. oligantha	2	1	?	1	?	1	1	0	2
C. ootensis	0	0	2	2	?	3	2	0	A
C. pallida	0	0&1	0	2	0	1	3	0	5
C. parvicalyx	0	1&2	1	2	0	1	3	0	6

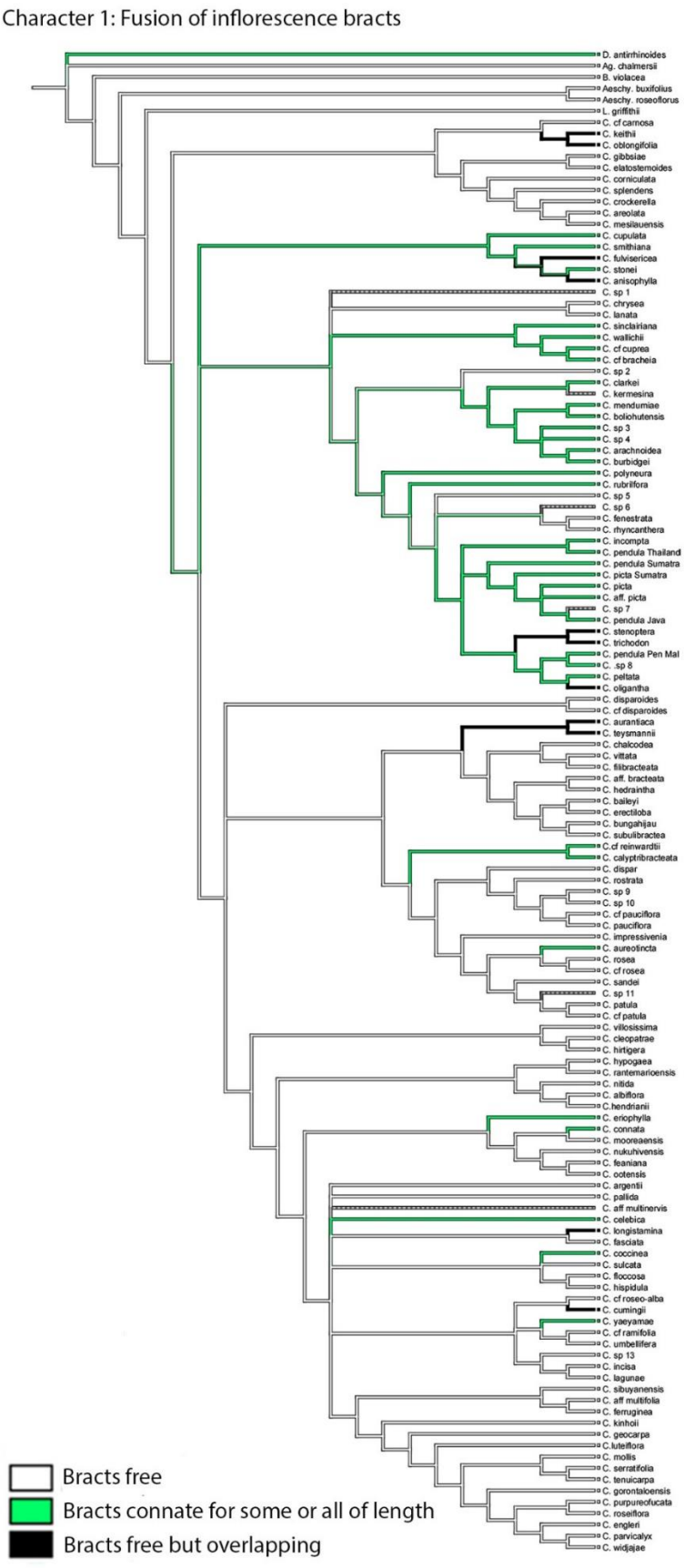
	Bracts	Leaves	Ovary	Habit	Disc	Fruit	Calyx	Corolla	Distribution
C. patula	0	0	1	2	1	3	1	0	0
C. pauciflora	0	1	?	2	?	1	3	0&1	2
C. peltata	1	1	?	1	0	3	1	0	2
C. pendula Java	1	1&2	0	1	0	1&3	1	0	3
C. pendula Pen Mal	1	1&2	0	1	0	1	5	0	0
C. pendula Sumatra	1	1&2	0	1	0	3	1	0	2
C. pendula Thailand	1	1&2	0	1	0	1	5	0	1
C. picta Java	1	0&1	0	1	0	1	1	0	3
C. picta Sumatra	1	0&1	0	1	0	1	1	0	2
C. polyneura	1	0	0	1	0	1	1	0	6
C. purpureofucata	0	0&1	1	2	0	3	3	1	6
C. rantemarioensis	0	0	1	2	1	3	3	1	6
C. rhyncanthera	0	0	2	1	0	1	3	0	2
C. rosea	0	0	1	2	1	3	3	1	2
C. roseiflora	0	0&1	1	2	0	1	3	1	6
C. rostrata	0	1	1	2	1	1	3	0	3
C. rubriflora	1	0	0	1	0	1	3	1	2
C. sandei	0	0	1	2	1	3	1	0&2	2&3
C. serratifolia	0	0	2	1&2	0	1	3	1	6
C. sibuyanensis	0	0	0	3	0	1	3	1	5
C. sinclairiana	1	0	0&1	1&2	0	1	6	0	4
C. smithiana	1	0	0	2	1	1	1	1	4
C. sp 1	?	0	?	1	?	1	?	0	4
C. sp 10	0	0	1	2	1	1	3	0	3
C. sp 11	?	0	?	2	?	3	?	?	2
C. sp 13	0	0	?	2	?	?	3	0	5
C. sp 2	0	0	1	1	0	1	3	0	5
C. sp 3	1	0	?	1	?	1	?	0	4
C. sp 4	1	0	?	1	?	1	?	0	4
C. sp 5	0	0	?	1	?	1	?	?	2
C. sp 6	?	0	?	1	?	?	?	?	2
C. sp 7	?	?	?	2	?	1	?	?	3
C. sp 8	1	1&2	0	1	0	1	5	0	2
C. sp 9	0	0	?	1	?	1	3	?	3
C. splendens	0	0	2	1&2	0	0	2	0	4
C. stenoptera	2	0	0	2	0	1	3	0	2
C. stonei	1	1	2	2	0	1&2	0	0	0
C. subulibractea	0	1	0	2	0	2	4	0&1&2	8&A
C. sulcata	0	0	1	2	1	1	3	0&1	3&6
C. tenuicarpa	0	0	2	1	0	0	3	0	6
C. teysmannii	2	0	?	2	?	1	1	1	2
C. trichodon	2	0	0	2	0	1	3	0	2
C. umbellifera	0	0	0	2	0	1	3	0	5&D

	Bracts	Leaves	Ovary	Habit	Disc	Fruit	Calyx	Corolla	Distribution
C. villosissima	0	0	1	2	0	1	2	1	5
C. vittata	0	0&1	0	1	0	3	3	1	8
C. wallichii	1	0	0&1	2	0	1	6	0	0&1
C. widjajae	0	1	1	2	0	3	3	0	6
C. yaeyamae	1	0	0	2	0	1	2	0	D
D. antirrhinoides	1	0	1&2	2	0	0	3	0&1&2	0
L. griffithii	0	0	?	1	?	0	2	1	B&C

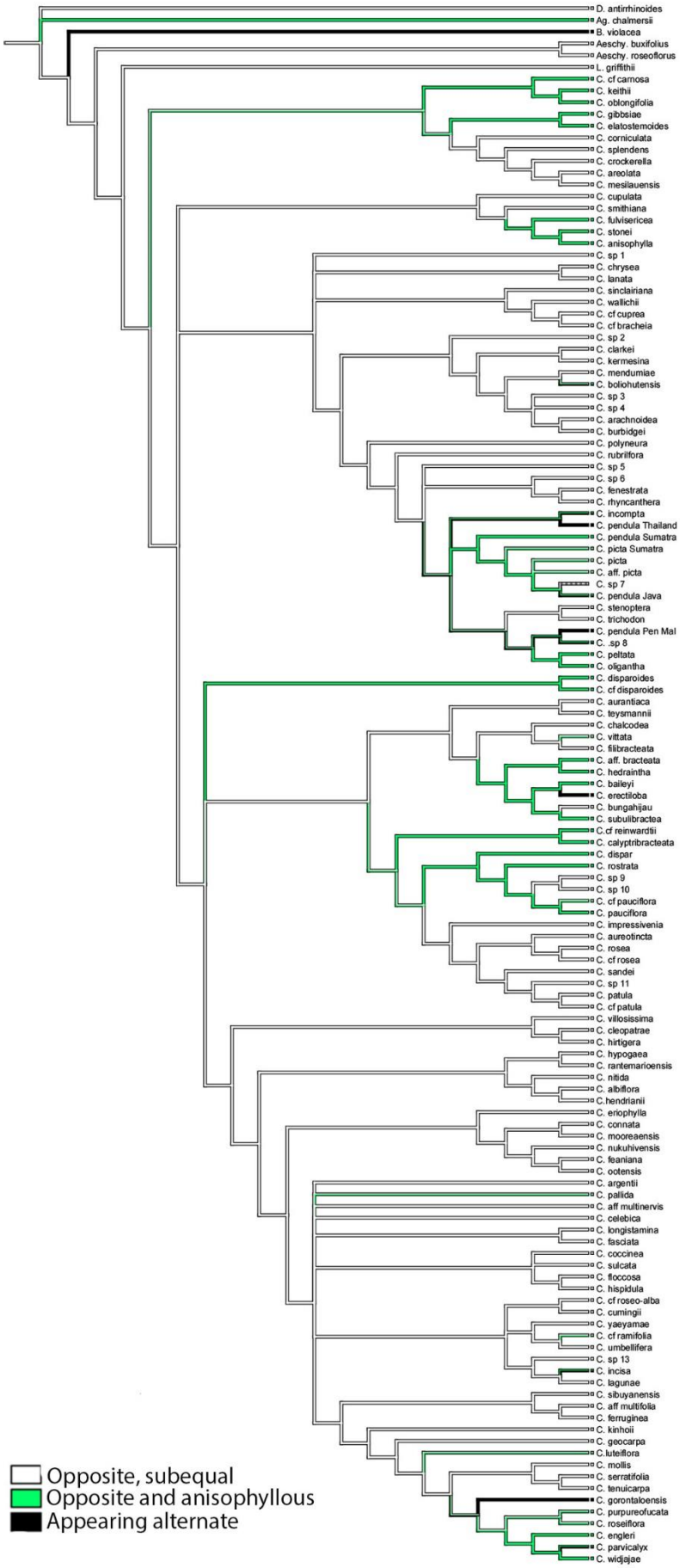
1. **Fusion of inflorescence bracts**: 0. Bracts free and not overlapping. 1. Bracts connate for some or all of their length. 2. Bracts free but overlapping, often forming a type of involucre.
2. **Leaf arrangement**: 0. Leaves opposite and subequal. 1. Leaves opposite and strongly anisophyllous. 2. Leaves appearing alternate.
3. **Ovary indumentum**: 0. Glabrous. 1. With a covering of eglandular hairs. 2. With a covering of sessile glands or glandular hairs.
4. **Habit**: 0. Epipyte. 1. Herb. 2. Shrub or small tree. 2. Climber (woody vine).
5. **Disc type**: 0. Cupular. 1. Unilateral.
6. **Fruit shape**: 0. Linear. 1. Ovoid. 2. Subglobose. 3. Oblong.
7. **Calyx type**: 0. Calyx in three parts. 1. Calyx tubular with very short lobes ie lobes less than 1/3 overall length of calyx. 2. Calyx with all lobes divided to base. 3. Calyx with some or all lobes divided to half way, often somewhat bilabiate. 4. Calyx spathulate, cleft to the base on one side to form one large lobe opposite a sinus. 5. Calyx with fewer than five lobes. 6. Calyx rupturing.
8. **Corolla base colour**: 0. White. 1. Red/ pink/ purple. 2. Yellow/ Orange 4. Green.
9. **Distribution**: 0. Peninsular Malaysia. 1. Thailand. 2. Sumatra. 3. Java. 4. Borneo. 5. Philippines. 6. Sulawesi. 7. Seram. 8. New Guinea. 9. Australia. 10 (A) Pacific. 11 (B) China. 12 (C) Vietnam. 13 (D) Japan and Taiwan.

NB. *C*. sp. 12 was not included in the character optimisation exercise as the specimen was not available for study.

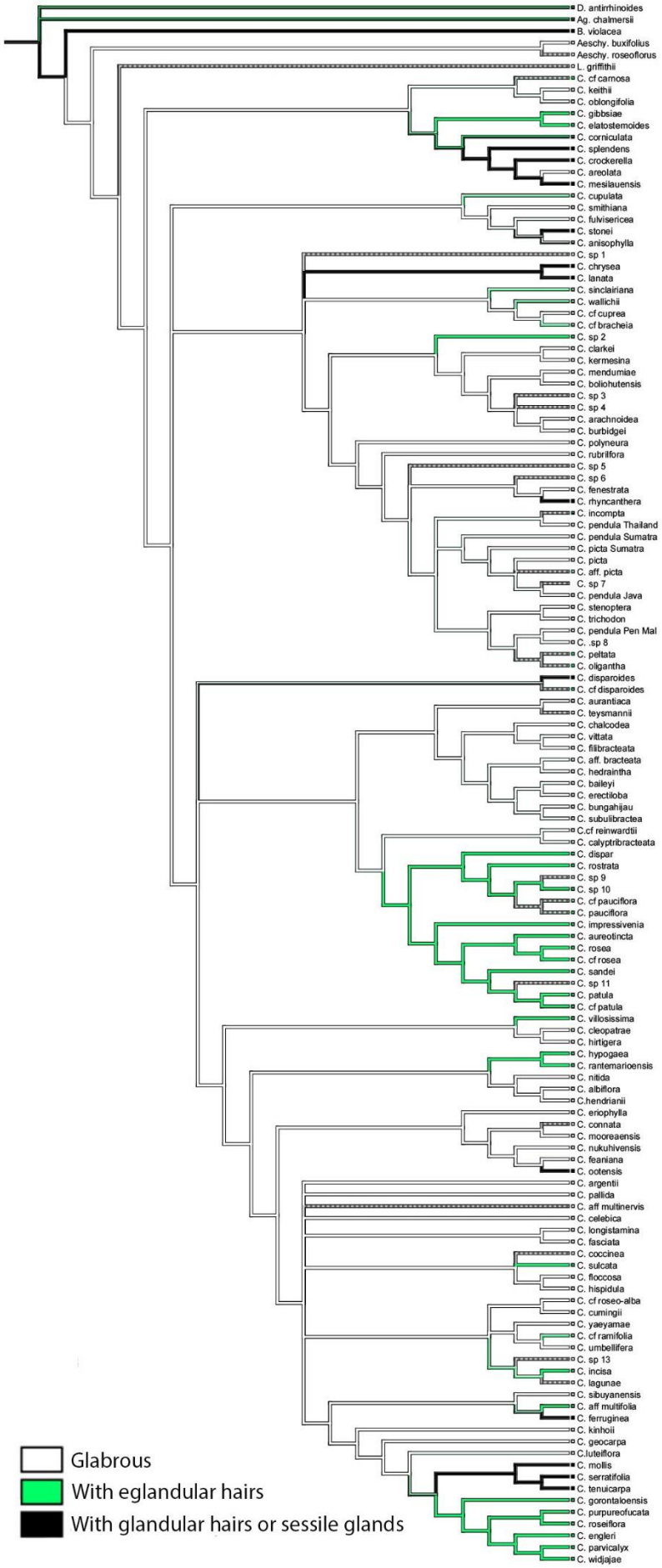
Appendix 3.3 Individual trees for the nine characters included in the Character Optimisation



Character 2: Leaf arrangement

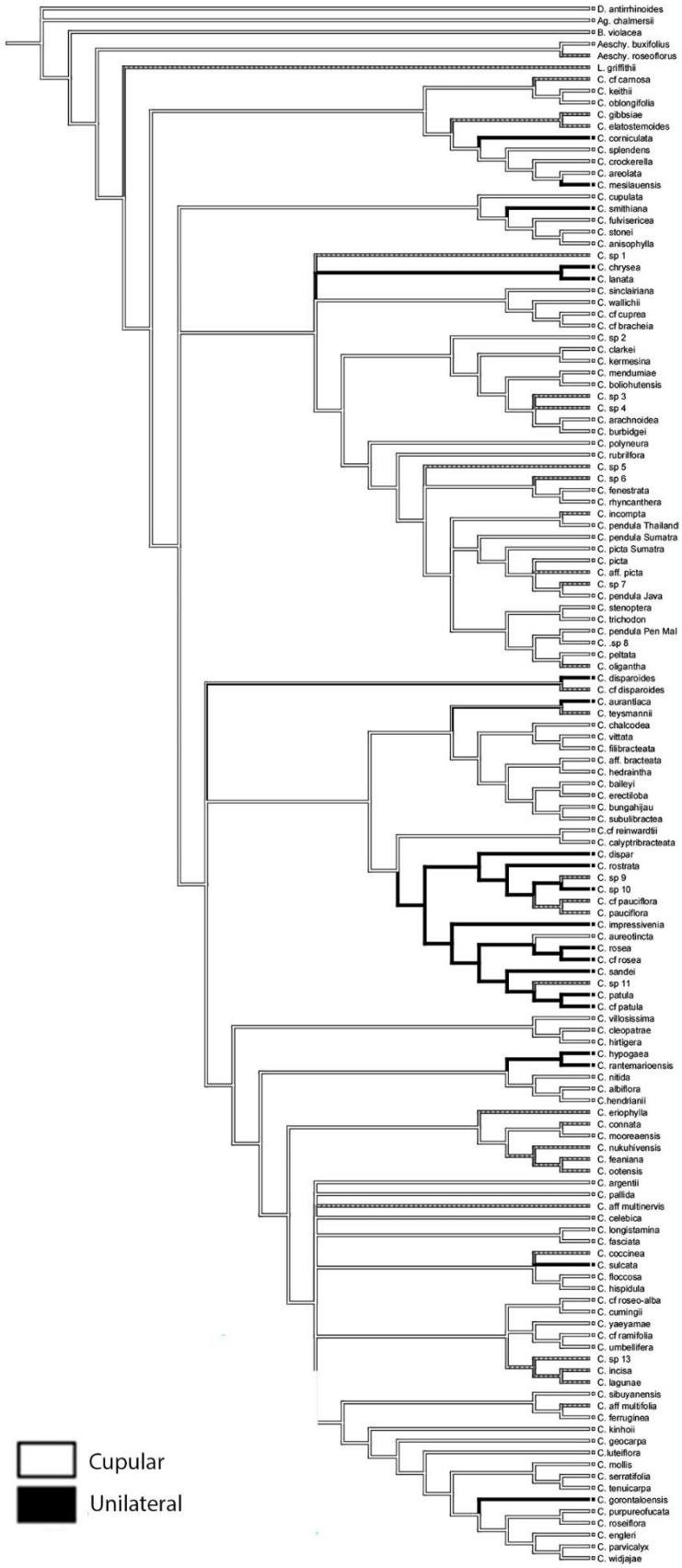


Character 3: Ovary indumentum

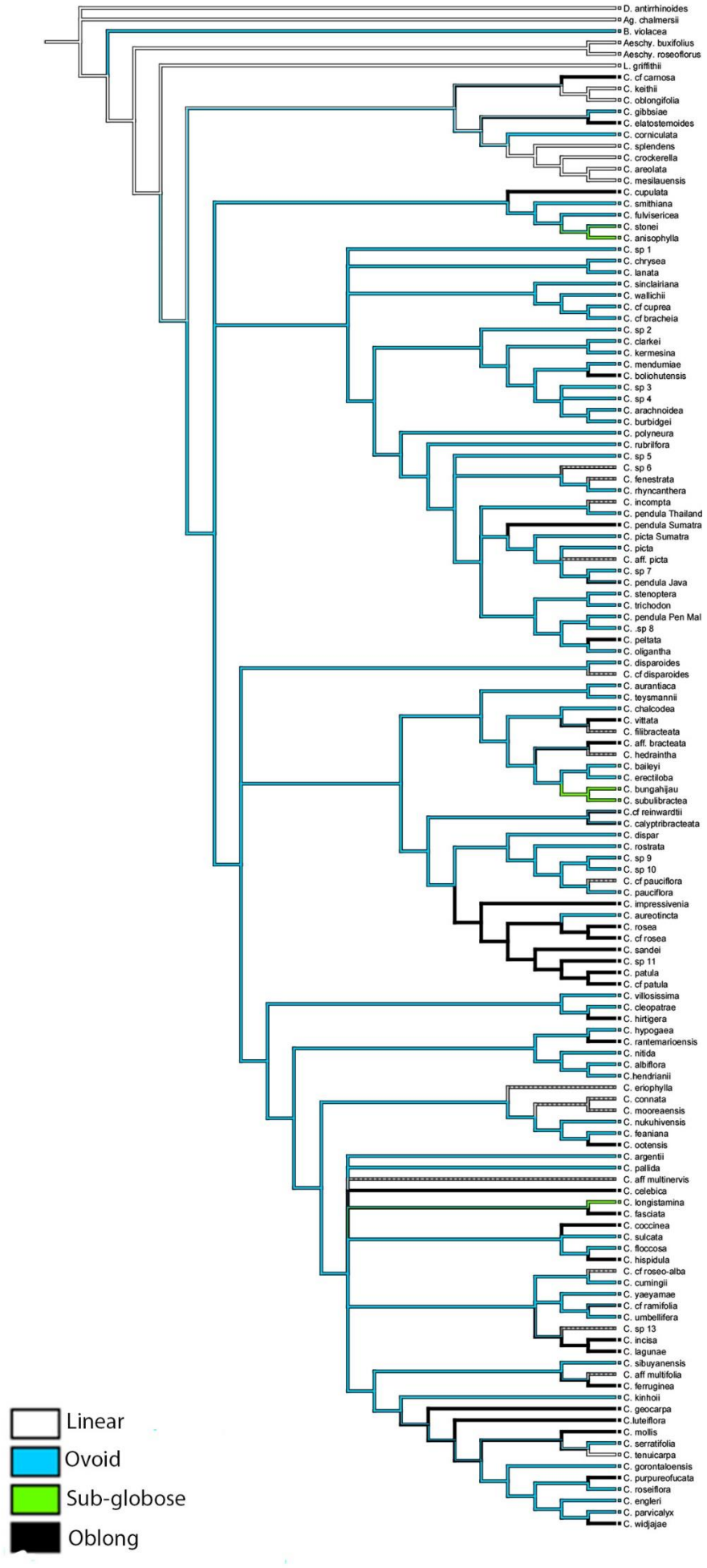


Character 4: Habit

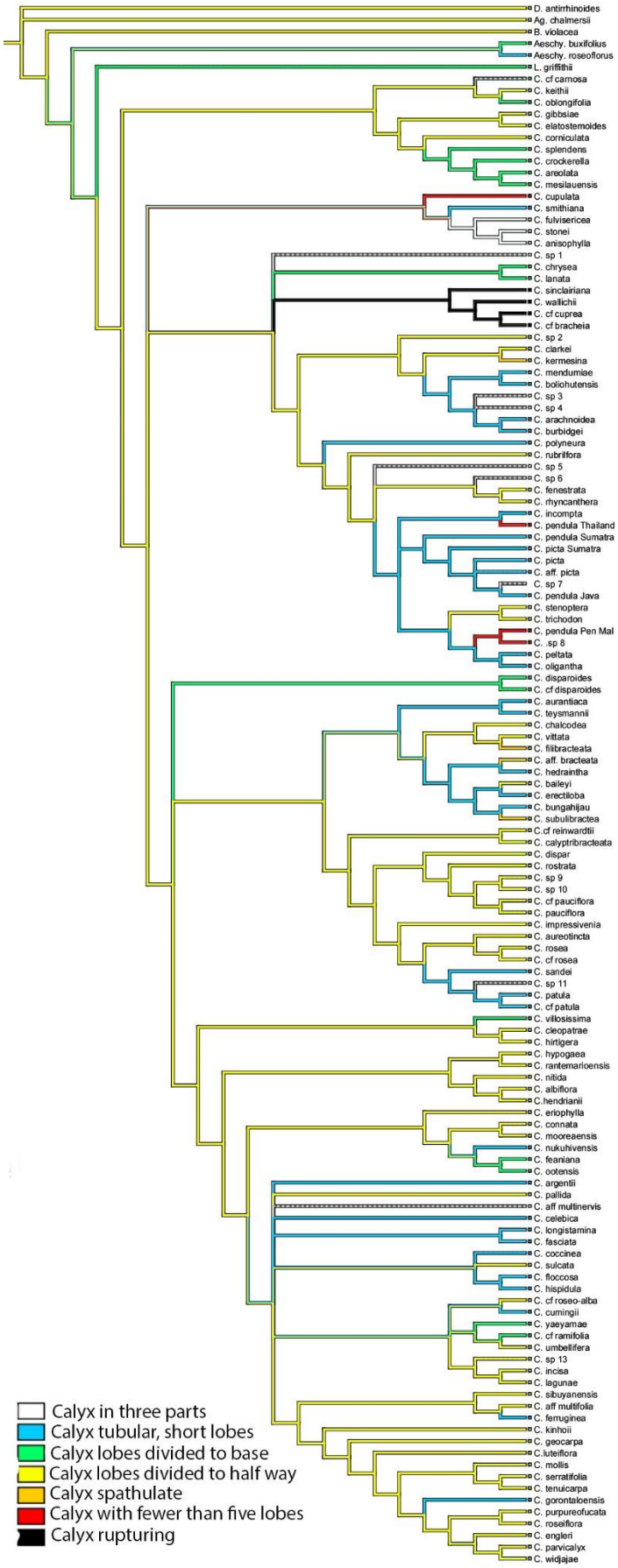
Character 5: Disc type



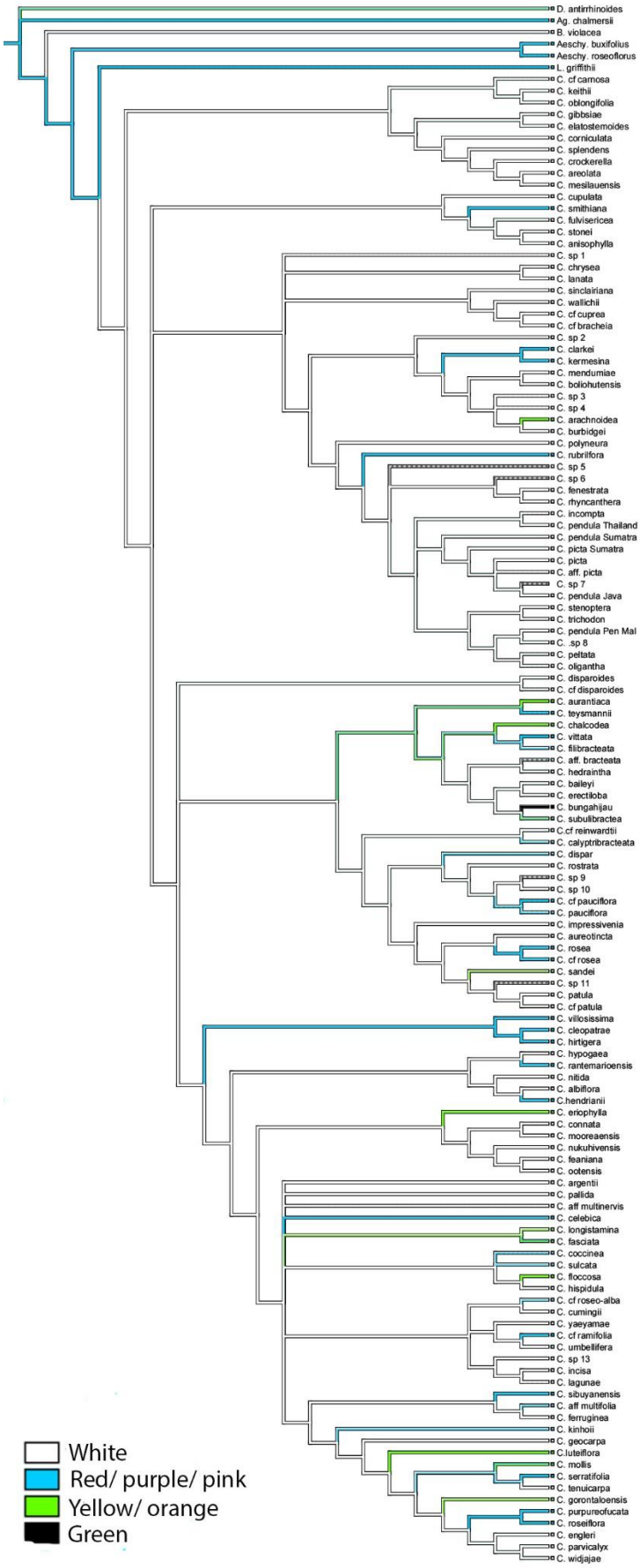
Character 6: Fruit shape



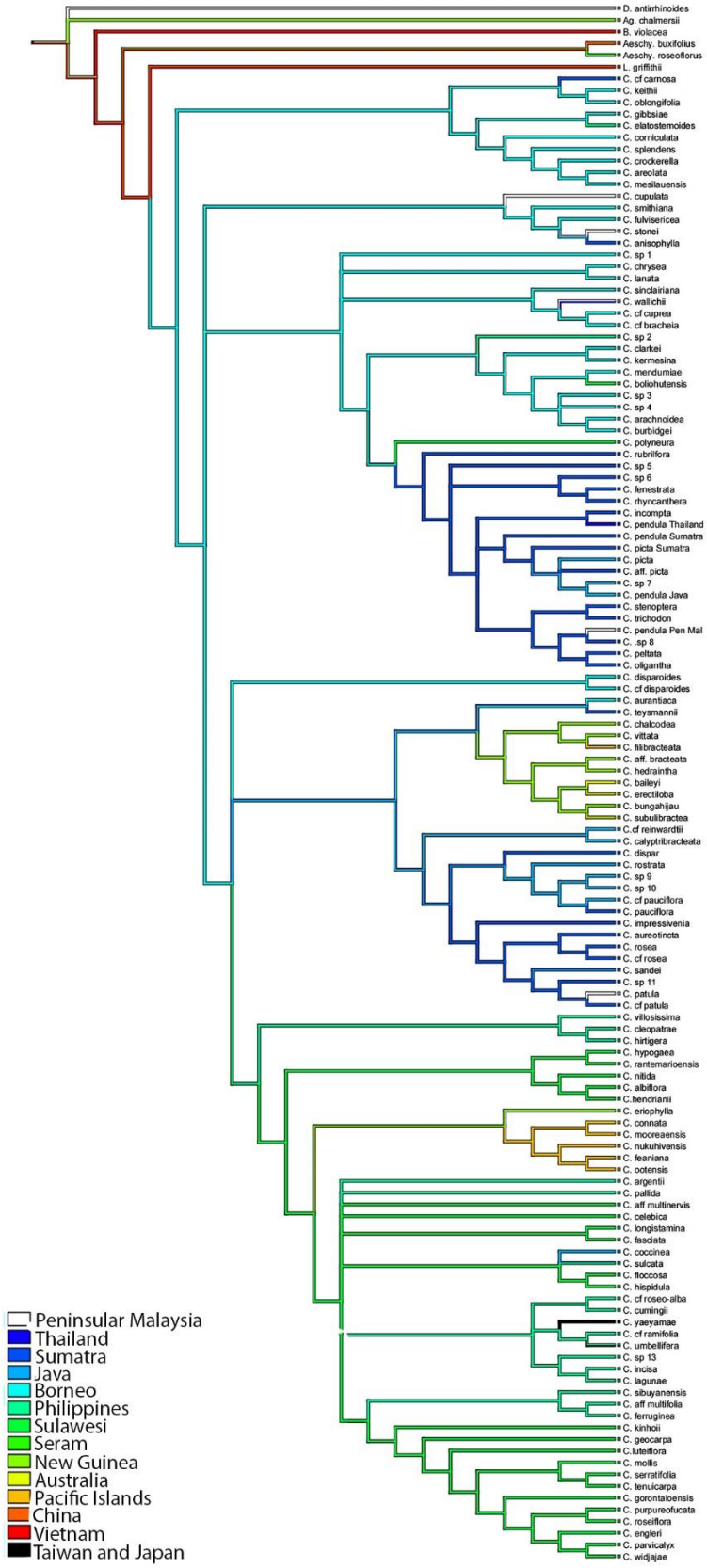
Character 7: Calyx type



Character 8: Corolla colour



Character 9: Distribution



Appendix 3.4 CI and RI scores for each of the characters included in the Character optimisation in Mesquite

Character	CI	RI
Fusion of bracts	0.9	0.55
Leaf arrangement	0.53	0.48
Ovary indumentum	0.43	0.58
Habit	0.47	0.6
Disc type	0.09	0.47
Fruit shape	0.22	0.33
Calyx type	0.16	0.46
Corolla colour	0.47	0.23
Distribution	0.44	0.72

Appendix 3.5 Taxon list for samples in the current study including six outgroup species. Ingroup samples are listed in alphabetical order by taxon name following the six outgroup taxa. Voucher details, locality and herbarium are given for each sample. GenBank accession numbers are included for each of the five genic regions. The * symbol indicates where no sequence data was obtained. Those sequencs generated by HA are in bold and italicised.

Species	Collector and Number	Herb	Locality	ITS	TrnLF	psbA-trnH	rpl32	matK
Aeschynanthus buxifolius	Goodwin & Cherry 384	E	Vietnam	MN843191	MN842996	MN843568	MN842817	MN843507
Aeschynanthus roseoflorus	Argent 87/14	E	Seram	MN843190	MN842995	MN843567	MN842816	MN843508
Agalmyla chalmersii	Chapman sn (RBGE acc no. 19661971)	E	New Guinea	MN843192	MN842997	MN843569	MN842818	MN843380
Billolivia violacea	South Vietnam First Darwin Expedition 201	E	Vietnam	MN843193	MN842994	MN843570	MN842819	*
Didymocarpus antirrinoides	Jong 9009 (RBGE acc no. 19650167)	E	Malaysia	MN843189	MN842994	MN843566	MN842815	MN843382
Loxostigma griffithii	Kew Edinburgh Kanchenjunga Expedition	E	Nepal	**MN843194**	**MN842999**	MN843571	MN842820	MN843509
C. aff *bracteata*	Utteridge 91	K	New Guinea	***MN843243***	***MN843049***	MN843616	MN842864	MN843427
C. aff *disparoides*	Wilkie et al SFC-07445	E	Borneo	***MN843211***	***MN843015***	MN843588	MN842837	MN843543
C. aff *erectiloba*	James 586	BISH	New Guinea	***MF446067***	***MN843060***	MF446277	MF509475	MN843546
C. aff *multinervis*	Argent et al 159	E	Sulawesi	***MN843292***	***MN843101***	MN843663	MN842910	MN843455
C. aff *picta*	Hughes et al SUBOE 78	E	Sumatra	***MN843349***	***MN843158***	MN843718	MN842965	MN843519
C. aff *ramiflora*	Mendum et al 29009	E	Philippines	***MN843269***	***MN843078***	*	*	MN843469
C. aff *rosea*	Hughes et al SUBOE 20	E	Sumatra	***MN843341***	***MN843150***	MN843710	MN842957	MN843513
C. aff *rosea*	Radhiah & Cronk 53	E	Sumatra	***MN843365***	***MN843174***	MN843734	*	MN843480
C. aff *rosea*	Radhiah & Cronk 55	E	Sumatra	***MN843366***	***MN843175***	MN843735	MN842981	MN843482
C. aff *ferruginea*	Mendum et al 29053	E	Philippines	***MN843273***	***MN843082***	MN843644	MN842893	MN843470
C. albiflora	Scott 509 (RBGE acc no 20040645)	E	Sulawesi	***MN843293***	***MN843102***	MN843664	*	MN843501
C. anisophylla	Radhiah & Cronk 109	E	Sumatra	***MN843335***	***MN843144***	MN843704	MN842952	MN843486
C. arachnoidea	Cronk, Burtt, Hilliard & Mendum CBHM 27	E	Borneo	***MN843197***	*	MN843573	MN842822	MN843451
C. areolata	Mendum, M. MM 52	E	Borneo	***MN843198***	***MN843001***	MN843574	MN842823	MN843420
C. aurantiaca	Cronk, Burtt, Hilliard & Mendum CBHM 23	E	Borneo	***MN843199***	***MN843002***	MN843575	MN842824	MN843496
C. aureotincta	Radhiah & Cronk 122	E	Sumatra	***MN843336***	***MN843145***	MN843705	MN842953	MN843491
C. baileyi	Cronk & Percy T118	E	Australia	***MN843195***	*	*	*	*
C. boliohutensis	Scott 505 (RBGE acc no 20021906)	E	Sulawesi	***MN843294***	***MN843103***	MN843665	MN842911	MN843384
C. boliohutensis	Argent et al 196	E	Sulawesi	***MN843295***	***MN843104***	MN843666	MN842912	MN843457
C. boliohutensis	Atkins et al 188	E	Sulawesi	***MN843296***	***MN843105***	MN843667	MN842913	MN843467
C. bungahijau	Atkins 57 (RBGE acc no 20090826)	E	New Guinea	***MN843249***	***MN843055***	MN843622	MN842870	MN843433
C. burbidgei	Cronk, Burtt, Hilliard & Mendum CBHM 21	E	Borneo	***MN843200***	***MN843003***	MN843576	MN842825	MN843449
C. burbidgei	Cronk, Burtt, Hilliard & Mendum CBHM 22	E	Borneo	***MN843201***	***MN843004***	MN843577	MN842826	MN843450
C. calyptribracteata	Moller sn (RBGE acc no 19973430)	E	Java	***MN843232***	***MN843036***	MN843605	MN842855	*
C. celebica	Thomas & Ardi 08-50	E	Sulawesi	***MN843297***	***MN843106***	MN843668	MN842914	MN843404

C. celebica	Argent et al 129	E	Sulawesi	***MN843298***	***MN843107***	MN843669	MN842915	MN843453
C. celebica	Barber et al BAKK 12	E	Sulawesi	***MN843300***	***MN843109***	MN843671	MN842917	MN843533
C. celebica	Barber et al BAKK 8	E	Sulawesi	***MN843299***	***MN843108***	MN843670	MN842916	MN843532
C. cf *bracheia*	Wilkie et al SFC-07447	E	Borneo	***MN843212***	***MN843016***	*	*	MN843558
C. cf *carnosa*	Girmansayah 17	E	Sumatra	***MN843355***	***MN843164***	MN843724	MN842971	MN843472
C. cf *cuprea*	Wilkie et al SFC-07404	E	Borneo	***MN843210***	***MN843014***	MN843587	MN842836	MN843542
C. cf *multifolia*	RBGE Philippines IS44	E	Philippines	***MN843268***	***MN843077***	MN843640	MN842889	MN843387
C. cf *patula*	Hughes et al SUBOE 12	E	Sumatra	***MN843337***	***MN843146***	MN843706	MN842954	*
C. cf *patula*	Hughes et al SUBOE 29	E	Sumatra	***MN843338***	***MN843147***	MN843707	MN842955	MN843515
C. cf *pauciflora*	Hoover ARS173	US	Java	***MN843234***	***MN843039***	MN843607	*	MN843544
C. cf *reinwardtii*	Wiriadanata 12709	US	Java	***MN843230***	***MN843034***	MN843603	MN842853	*
C. cf *roseo-alba*	Cronk MAK1	E	Philippines	***MN843267***	***MN843076***	MN843639	MN842888	MN843399
C. chalcodea	James 1232	BISH	New Guinea	***MN843252***	***MN843058***	MN843624	MN842873	MN843505
C. chrysea	Mendum MM58	E	Borneo	***MN843206***	***MN843009***	MN843583	MN842832	MN843421
C. clarkei	Cronk, Burtt, Hilliard & Mendum CBHM 19	E	Borneo	***MF446060***	***MN843010***	MF446268	MF509462	MN843381
C. cleopatrae	Cronk et al 25437	E	Philippines	***MN843274***	***MN843083***	MN843645	*	MN843468
C. coccinea	Hoover ARS167	US	Java	***EU919972***	***MN843037***	GQ475131	MF509463	MN843550
C. connata	Cronk & Percy T92	E	Society Is	***MN843259***	***MN843068***	MN843631	MN842880	MN843393
C. connata	Cronk & Percy T93	E	Society Is	***MN843260***	***MN843069***	MN843632	MN842881	*
C. corniculata	Cronk, Burtt, Hilliard, Mendum CBHM 9	E	Borneo	***MN843207***	***MN843011***	MN843584	MN842833	MN843400
C. crockerella	Mendum MM 43	E	Borneo	***MN843208***	***MN843012***	MN843585	MN842834	MN843417
C. cumingii	RBGE Philippines 99206	E	Philippines	***MN843278***	***MN843087***	MN843649	*	MN843395
C. cupulata	Atkins 59 (RBGE acc no 20010490)	E	Peninsular Malaysia	***MN843282***	***MN843091***	MN843653	MN842900	MN843436
C. cupulata	Phoon FRI53377	BKF	Peninsular Malaysia	***MN843283***	***MN843092***	MN843654	MN842901	MN843471
C. cupuluta	Bramley et al GB28	E	Peninsular Malaysia	***MN843284***	***MN843093***	MN843655	MN842902	MN843424
C. dispar	Wilkie PW 642	E	Sumatra	***MN843342***	***MN843151***	MN843711	MN842958	MN843392
C. dispar	Puglisi et al CP 247	E	Sumatra	***MN843344***	***MN843153***	MN843713	MN842960	MN843443
C. dispar	Radhiah & Cronk 58	E	Sumatra	***MN843345***	***MN843154***	MN843714	MN842961	MN843483
C. dispar	Hughes et al SUBOE 13	E	Sumatra	***MN843347***	***MN843156***	MN843716	MN842963	MN843512
C. disparoides	Church 292	E	Borneo	***MN843209***	***MN843013***	MN843586	MN842835	MN843498
C. elatostemmoides	Puglisi CP302	E	Philippines	***MN843275***	***MN843084***	MN843646	MN842894	MN843414
C. engleri	Scott & Cubey 228 (RBGE acc no 20021223)	E	Sulawesi	***MN843290***	***MN843099***	MN843661	MN842908	MN843434
C. engleri	Atkins et al 202	E	Sulawesi	***MN843291***	***MN843100***	MN843662	MN842909	MN843499
C. erectiloba	James 134	BISH	New Guinea	***MF446066***	***MN843059***	MF446275	MF509473	MN843545
C. eriophylla	Sands 7158	K	New Guinea	***MN843241***	***MN843047***	MN843614	MN842862	MN843425

C. eriophylla	Johns 10040	K	New Guinea	***MN843242***	***MN843048***	MN843615	MN842863	MN843426
C. eriophylla	Utteridge 162	K	New Guinea	***MN843244***	***MN843050***	MN843617	MN842865	MN843428
C. eriophylla	Argent 533	E	New Guinea	***MN843250***	***MN843056***	MN843623	MN842871	MN843503
C. fasciata	Argent et al 198	E	Sulawesi	***MN843303***	***MN843112***	MN843674	MN842920	MN843459
C. fasciata	Atkins et al 54	E	Sulawesi	***MN843304***	***MN843113***	MN843675	MN842921	MN843464
C. feaniana	Percy CM1	E	Marquesas	***MN843255***	***MN843064***	MN843627	MN842876	MN843411
C. fenestrata	Radhiah & Cronk 147	E	Sumatra	***MN843351***	***MN843160***	MN843720	MN842967	MN843555
C. ferruginea	Cubey & Scott 226 (RBGE acc no 19972533)	E	Philippines	***MN843270***	***MN843079***	MN843641	MN842890	MN843437
C. filibracteata	James 1770	BISH	Solomon Islands	***MN843258***	***MN843067***	MN843630	MN842879	MN843564
C. floccosa	Thomas & Ardi 09-90	E	Sulawesi	***MN843305***	***MN843114***	MN843676	MN842922	MN843406
C. fulvisericea	Cronk, Burtt, Hilliard & Mendum CBHM 13	E	Borneo	***MN843213***	***MN843017***	MN843589	MN842838	MN843447
C. fulvisericea	Cronk, Burtt, Hilliard & Mendum CBHM 16	E	Borneo	***MN843214***	***MN843018***	MN843590	MN842839	MN843448
C. geocarpa	Atkins 12 (RBGE acc no 20021222)	E	Sulawesi	***MN843306***	***MN843115***	MN843677	MN842923	MN843388
C. geocarpa	Barber et al BAKK 25	E	Sulawesi	***MN843307***	***MN843116***	MN843678	MN842924	*
C. gibbsiae	Cronk, Burtt, Hilliard, Mendum CBHM 11	E	Borneo	***MN843215***	***MN843019***	MN843591	MN842840	MN843401
C. gibbsiae	Mendum, M. MM 61	E	Borneo	***MN843216***	***MN843020***	MN843592	MN842841	MN843548
C. gorontaloensis	Barber et al BAKK 68	E	Sulawesi	***MN843302***	***MN843111***	MN843673	MN842919	MN843540
C. gorontaloensis	Atkins et al 91	E	Sulawesi	***MN843308***	***MN843117***	MN843679	MN842925	MN843466
C. hedraiantha	de Kok 1239	K	New Guinea	***MN843246***	***MN843052***	MN843619	MN842867	MN843430
C. hendrianii	Scott 503 (RBGE acc no 20040646)	E	Sulawesi	***MN843309***	***MN843118***	MN843680	MN842926	MN843500
C. hirtigera	Cronk et al 25518	E	Philippines	***MN843276***	***MN843085***	MN843647	MN842895	MN843556
C. hirtigera	Cronk et al 25433	E	Philippines	***MN843277***	***MN843086***	MN843648	MN842896	MN843549
C. hispidula	Thomas & Ardi 09-86	E	Sulawesi	***MN843310***	***MN843119***	MN843681	MN842927	*
C. hypogaea	Scott 449 (RBGE acc no 20040647)	E	Sulawesi	***MN843311***	***MN843120***	MN843682	MN842928	MN843383
C. hypogaea	Barber et al BAKK 17	E	Sulawesi	***MN843312***	***MN843121***	*	MN842929	MN843534
C. impressivenia	Radhiah & Cronk 116	E	Sumatra	***MN843352***	***MN843161***	MN843721	MN842968	MN843490
C. incisa	Cronk MAK4	E	Philippines	***MN843271***	***MN843080***	MN843642	MN842891	MN843445
C. incompta	Radhiah & Cronk 50	E	Sumatra	***MN843353***	***MN843162***	MN843722	MN842969	MN843479
C. keithii	Bramley et al SAN147235	K	Borneo	***MN843218***	*	MN843581	MN842830	MN843526
C. kermesina	Cronk, Burtt, Hilliard & Mendum CBHM 8	E	Borneo	***MN843217***	***MN843021***	MN843593	MN842842	MN843446
C. kermesina	Cronk, Burtt, Hilliard & Mendum CBHM 14	E	Borneo	***MN843219***	***MN843022***	MN843594	MN842843	MN843494
C. kinhoi	Atkins et al 56	E	Sulawesi	***MN843313***	***MN843122***	MN843683	MN842930	MN843465
C. kinhoi	Barber et al BAKK 36	E	Sulawesi	***MN843314***	***MN843123***	MN843684	MN842931	MN843536
C. kinhoi	Barber et al BAKK 65	E	Sulawesi	***MN843315***	***MN843124***	*	MN842932	MN843539

C. lagunae	Cronk MAK3	E	Philippines	***MN843272***	***MN843081***	MN843643	MN842892	MN843444
C. lanata	Cronk, Burtt, Hilliard & Mendum CBHM 20	E	Borneo	***MN843220***	***MN843023***	*	*	MN843495
C. longistamina	Argent et al 197	E	Sulawesi	***MN843301***	***MN843110***	MN843672	MN842918	MN843458
C. luteiflora	Atkins et al 52	E	Sulawesi	***MN843316***	***MN843125***	MN843685	MN842933	MN843463
C. mendumiae	Mendum MM 46	E	Borneo	***MN843221***	***MN843024***	MN843595	MN842844	MN843419
C. mesilauensis	Cronk, Burtt, Hilliard, Mendum CBHM 7	E	Borneo	***MN843222***	***MN843025***	*	MN842845	MN843402
C. mesilauensis	Cronk, Burtt, Hilliard & Mendum CBHM 6	E	Borneo	***MF446095***	***MN843026***	MN843596	MN842846	MN843493
C. mollis	Barber et al BAKK 42	E	Sulawesi	***MN843317***	***MN843126***	MN843686	MN842934	MN843557
C. mollis	Barber et al BAKK 83	E	Sulawesi	***MN843318***	***MN843127***	MN843687	MN842935	MN843541
C. mooreaensis	Cronk & Percy T26	E	Society Is	***MN843261***	***MN843070***	MN843633	MN842882	*
C. nitida	Argent et al 111	E	Sulawesi	***MN843319***	***MN843128***	MN843688	MN842936	MN843452
C. nukuhivensis	Percy CM4	E	Marquesas	***MN843256***	***MN843065***	MN843628	MN842877	MN843413
C. oblongifolia	Scott 506 (RBGE acc no 19912412)	E	Borneo	***MN843223***	***MN843027***	MN843597	MN842847	MN843415
C. oligantha	Radhiah & Cronk 68	E	Sumatra	***MN843356***	***MN843165***	MN843725	MN842972	MN843422
C. oligantha	Radhiah & Cronk 54	E	Sumatra	***MN843357***	***MN843166***	MN843726	MN842973	MN843481
C. oligantha	Hughes et al SUBOE 10	E	Sumatra	***MN843358***	***MN843167***	MN843727	MN842974	MN843511
C. ootensis	Percy CM3	E	Marquesas	***MN843257***	***MN843066***	MN843629	MN842878	MN843412
C. pallida	RBGE Philippines 99219	E	Philippines	***MN843279***	***MN843088***	MN843650	MN842897	MN843396
C. patula	Bramley et al GB36	E	Peninsular Malaysia	***MN843285***	***MN843094***	MN843656	MN842903	MN843478
C. pauciflora	Hughes et al SUBOE 70	E	Sumatra	***MN843339***	***MN843148***	MN843708	*	MN843517
C. pauciflora	Hughes et al SUBOE 72	E	Sumatra	***MN843340***	***MN843149***	MN843709	MN842956	MN843518
C. peltata	Radhiah & Cronk 71	E	Sumatra	***MN843359***	***MN843168***	MN843728	MN842975	MN843484
C. pendula	Atkins 4	E	Java	***MN843235***	***MN843040***	MN843608	MN842857	MN843439
C. pendula	Bramley et al GB37	E	Peninsular Malaysia	***MN843286***	***MN843095***	MN843657	MN842904	MN843565
C. pendula	Radhiah & Cronk 74	E	Sumatra	***MN843360***	***MN843169***	MN843729	MN842976	MN843552
C. pendula	Hughes et al SUBOE 28	E	Sumatra	***MN843361***	***MN843170***	MN843730	MN842977	MN843514
C. pendula	Middleton et al 5447	E	Thailand	***MN843373***	***MN843182***	MN843742	MN842988	MN843441
C. pendula	Middleton et al 3950	E	Thailand	***MN843374***	***MN843183***	MN843743	MN842989	MN843442
C. pendula	Poopath MP60	BKF	Thailand	***MN843375***	***MN843184***	MN843744	MN842990	MN843474
C. pendula	Wilkie PW925	E	Thailand	***MN843376***	***MN843185***	MN843745	*	MN843506
C. picta	Radhiah & Cronk 66	E	Java	***MN843236***	***MN843041***	MN843609	MN842858	MN843553
C. picta	Atkins 2	E	Java	***MN843237***	***MN843042***	MN843610	MN842859	MN843438
C. picta	Radhiah & Cronk 108	E	Sumatra	***MN843354***	***MN843163***	MN843723	MN842970	MN843485
C. polyneura	Thomas & Ardi 08-25	E	Sulawesi	***MN843320***	***MN843129***	MN843689	MN842937	MN843403
C. polyneura	Argent et al 217	E	Sulawesi	***MN843321***	***MN843130***	MN843690	MN842938	MN843561
C. polyneura	Atkins et al 40	E	Sulawesi	***MN843322***	***MN843131***	MN843691	MN842939	MN843462
C. polyneura	Barber et al BAKK 41	E	Sulawesi	***MN843323***	***MN843132***	MN843692	MN842940	MN843537
C. purpureofucata	Thomas & Ardi 09-88	E	Sulawesi	***MN843324***	***MN843133***	MN843693	MN842941	MN843405

C. purpureofucata	Argent et al 252	E	Sulawesi	***MN843325***	***MN843134***	MN843694	MN842942	MN843461
C. rantemarioensis	Thomas & Ardi 09-81	E	Sulawesi	***MN843326***	***MN843135***	MN843695	MN842943	MN843407
C. rantemarioensis	Thomas & Ardi 09-79	E	Sulawesi	***MN843327***	***MN843136***	MN843696	MN842944	MN843408
C. rantemarioensis	Argent et al 240	E	Sulawesi	***MN843328***	***MN843137***	MN843697	MN842945	MN843460
C. rhyncanthera	Radhiah & Cronk 111	E	Sumatra	***MN843362***	***MN843171***	MN843731	MN842978	MN843488
C. rosea	Radhiah & Cronk 115	E	Sumatra	***MN843363***	***MN843172***	MN843732	MN842979	*
C. roseiflora	Argent et al 173	E	Sulawesi	***MN843329***	***MN843138***	MN843698	MN842946	MN843456
C. rostrata	Radhiah & Cronk 162	E	Java	***MN843238***	***MN843043***	MN843611	*	MN843410
C. rubriflora	Wilkie PW 603	E	Sumatra	***MN843364***	***MN843173***	MN843733	MN842980	MN843391
C. sandei	Atkins 5	E	Java	***MN843239***	***MN843044***	MN843612	MN842860	MN843440
C. sandei	Hughes et al SUBOE 93	E	Sumatra	***MN843367***	***MN843176***	MN843736	MN842982	MN843520
C. sect. *Geodesme*	de Kok 1266	K	New Guinea	***MN843248***	***MN843054***	MN843621	MN842869	MN843432
C. sect. *Geodesme*	Argent 609	E	New Guinea	***MN843251***	***MN843057***	*	MN842872	MN843504
C. serratifolia	Atkins et al 93	E	Sulawesi	***MN843330***	***MN843139***	MN843699	MN842947	*
C. serratifolia	Barber et al BAKK 44	E	Sulawesi	***MN843331***	***MN843140***	MN843700	MN842948	MN843538
C. sibuyanensis	RBGE Philippines 99218	E	Philippines	***MN843280***	***MN843089***	MN843651	MN842898	MN843397
C. sinclairiana	Cronk, Burtt, Hilliard, Mendum CBHM 1	E	Borneo	***MN843224***	***MN843028***	MN843598	MN842848	*
C. smithiana	Mendum MM30	E	Borneo	***MN843225***	***MN843029***	MN843599	MN842849	MN843418
C. smithiana	Bramley et al SAN147245	E	Borneo	***MN843205***	***MN843008***	MN843582	MN842831	MN843525
C. smithiana	Cronk, Burtt, Hilliard & Mendum CBHM 25	E	Borneo	***MN843226***	***MN843030***	MN843600	MN842850	MN843497
C. sojolensis	Argent et al 158	E	Sulawesi	***MN843332***	***MN843141***	MN843701	MN842949	MN843454
C. sp 1	Bramley et al SAN147207	K	Borneo	***MN843203***	***MN843006***	MN843579	MN842828	MN843524
C. sp 2	RBGE Philippines 99211	E	Philippines	***MN843281***	***MN843090***	MN843652	MN842899	MN843398
C. sp 3	Bramley et al SAN147205	K	Borneo	***MN843202***	***MN843005***	MN843578	MN842827	MN843523
C. sp 4	Bramley et al SAN147222	K	Borneo	***MN843204***	***MN843007***	MN843580	MN842829	MN843527
C. sp 5	Hughes et al SUBOE 9	E	Sumatra	***MN843346***	***MN843155***	MN843715	MN842962	MN843510
C. sp 6	Hughes et al SUBOE 41	E	Sumatra	***MN843348***	***MN843157***	MN843717	MN842964	MN843516
C. sp 7	Wiriadanata 12713	US	Java	***MN843231***	***MN843035***	MN843604	MN842854	MN843522
C. sp 8	Wilkie PW 760	E	Sumatra	***MN843343***	***MN843152***	MN843712	MN842959	MN843390
C. sp 9	Argent & Smith 11	E	Bali	***MN843196***	***MN843000***	MN843572	MN842821	MN843502
C. sp 10	Radhiah & Cronk 168	E	Java	***MN843233***	***MN843038***	MN843606	MN842856	MN843409
C. sp 11	Hughes et al SUBOE 96	E	Sumatra	***MN843350***	***MN843159***	MN843719	MN842966	MN843521
C. sp 12	Kiehn 940808	W	Hawaii	***MN843254***	***MN843063***	MN843626	MN842875	MN843394
C. splendens	Clark 820		Borneo	***MN843227***	***MN843031***	*	*	MN843559
C. stenoptera	Radhiah & Cronk 145	E	Sumatra	***MN843368***	***MN843177***	MN843737	MN842983	MN843423
C. stenoptera	Radhiah & Cronk 110	E	Sumatra	***MN843369***	***MN843178***	MN843738	MN842984	MN843487
C. stenoptera	Radhiah & Cronk 113	E	Sumatra	***MN843370***	***MN843179***	MN843739	MN842985	MN843489
C. stonei	Bramley et al GB34	E	Peninsular Malaysia	***MN843287***	***MN843096***	MN843658	MN842905	MN843477

C. subulibractea	James 408	BISH	New Guinea	***MN843253***	***MN843061***	MN843625	MN842874	MN843563
C. subulibractea	James 445	BISH	New Guinea	***MF446138***	***MN843062***	MF446344	MF509567	MN843547
C. sulcata	Hoover ARS160	US	Java	***EU919980***	***MN843045***	GQ475132	MF509569	MN843551
C. tenuicarpa	Argent et al 229	E	Sulawesi	***MN843333***	***MN843142***	MN843702	MN842950	MN843560
C. teysmannii	Radhiah & Cronk 87	E	Sumatra	***MN843371***	***MN843180***	MN843740	MN842986	MN843562
C. trichodon	Radhiah & Cronk 124	E	Sumatra	***MN843372***	***MN843181***	MN843741	MN842987	MN843492
C. umbellifera	Kokubugata GK15859	TNS	Philippines	***MN843265***	***MN843074***	MN843637	MN842886	MN843530
C. umbellifera	Kokubugata GK6031	TNS	Taiwan	***MN843379***	***MN843188***	MN843748	MN842993	MN843528
C. villosissima	CULTE 16108 (RBGE acc no 19991945)	E	Philippines	***MN843264***	***MN843073***	MN843636	MN842885	MN843416
C. villosissima	RBGE Philippines 99316	E	Philippines	***MN843266***	***MN843075***	MN843638	MN842887	MN843554
C. vittata	Atkins 14 (RBGE acc no 20090734)	E	New Guinea	***MN843240***	***MN843046***	MN843613	MN842861	MN843385
C. vittata	de Kok 1156	K	New Guinea	***MN843245***	***MN843051***	MN843618	MN842866	MN843429
C. vittata	de Kok 1263	K	New Guinea	***MN843247***	***MN843053***	MN843620	MN842868	MN843431
C. wallichii	Bramley et al GB25	E	Peninsular Malaysia	***MN843288***	***MN843097***	MN843659	MN842906	MN843475
C. wallichii	Bramley et al GB33	E	Peninsular Malaysia	***MN843289***	***MN843098***	MN843660	MN842907	MN843476
C. wallichii	Atkins 41 (RBGE acc no 20090366)	E	Thailand	***MN843377***	***MN843186***	MN843746	MN842991	MN843389
C. wallichii	Poopath MP187	BKF	Thailand	***MN843378***	***MN843187***	MN843747	MN842992	MN843473
C. widjajae	Barber et al BAKK 32	E	Sulawesi	***MN843334***	***MN843143***	MN843703	MN842951	MN843535
C. yaeyamae	Kokubugata GK18916	TNS	Japan	***MN843229***	***MN843033***	MN843602	MN842852	MN843531
C. yaeyamae	Scott 501 (RBGE acc no 20031648A)	E	Japan	***MN843263***	***MN843072***	MN843635	MN842884	MN843386

Chapter Four: A molecular phylogeny of Southeast Asian *Cyrtandra* (Gesneriaceae) supports an emerging paradigm for Malesian plant biogeography

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Abstract

The islands of Southeast Asia comprise one of the most geologically and biogeographically complex areas in the world and are a centre of exceptional floristic diversity, harbouring 45,000 species of flowering plants. *Cyrtandra* is the largest genus in the family Gesneriaceae with over 800 species of herbs and shrubs, and is one of the most emblematic and species-rich genera of the Malesian rainforest understorey. The high number of species and tendency to narrow endemism make *Cyrtandra* an ideal genus for examining biogeographic patterns. We sampled 128 *Cyrtandra* taxa from key localities across Southeast Asia to evaluate the geo-temporal patterns and evolutionary dynamics of this radiation. One nuclear and four chloroplast regions were used for phylogenetic reconstruction, molecular dating, and ancestral range estimation. Results from the dating analysis suggests that the great diversity of *Cyrtandra* seen in the Malesian region results from a recent diversification, with most speciation taking place in the last five million years. Borneo was recovered as the ancestral range of the genus, with the current distribution of species resulting from a west to east migration across Malesia that corresponds with island emergence and mountain building. Lastly, our investigation into the biogeographic history of the genus indicates high levels of floristic exchange between the islands on the Sunda shelf. These patterns underlie much of the plant diversity in the region and form an emerging paradigm in Southeast Asian plant biogeography.

Keywords

Wallacea, Sunda shelf, Sahul shelf, floristic exchange, molecular dating, ancestral range estimation, biogeographic stochastic mapping, recent divergence, island biogeography

Running title

A molecular phylogeny of Southeast Asian *Cyrtandra*

4.1 Introduction

The islands of Southeast Asia comprise one of the most geologically and biogeographically complex areas in the world (Hall, 2002, Gower et al., 2012, Lohman et al., 2011) and are the meeting and mixing point of floras and faunas of diverse origins (van Welzen et al. 2011; Richardson et al. 2012). The area is highly diverse, estimated to harbour approximately 45,000 species of vascular plants on more than 20,000 islands (Lohman et al., 2011). It contains the biodiversity hotspots of Sundaland, Wallacea and the Philippines (Myers et al., 2002, Brooks et al., 2006) and the mega-diverse island of New Guinea (Mittermeier et al., 2003, Takeuchi, 2005, Hoover et al. 2017).

The region has been of interest to biogeographers since Wallace's seminal papers on faunal distribution patterns and physical geography of the region (Wallace, 1860, 1863) and is regarded by many as the birthplace of modern biogeography (Lohman et al., 2011) and, indeed, evolution (van Whye, 2012). Wallace's prescient idea that past geological connections and biotic migrations have an impact on current distribution patterns has largely been proved to be correct as our understanding of the underlying mechanisms and the geological and climatological backdrop against which these have played out has improved.

The geological history of the Malesian region is a complex and intricate mosaic of islands of different origins and types that has undergone a tumultuous and dynamic history over the last 50 million years (my) (Hall, 2002, Hall, 2012a,b). In the west of the region are the continental Sunda shelf islands of Sumatra, Java and Borneo, separated by shallow seas; in the centre are the numerous smaller terranes and oceanic islands that comprise the Philippines and Wallacea, and in the east is the Sahul shelf and the large island of New Guinea which is itself of composite origin. Adding a layer of complexity to this is the changing climate of the past 50 my (Morley, 2012, 2018), most strikingly the fluctuating glacials and interglacials of the Pleistocene (Woodruff, 2010, Morley, 2012) which impacted sea levels and the extent of vegetation types (Woodruff, 2010, Cannon, 2012, Morley, 2012, Cannon et al., 2014).

Over the last decade, an increasing number of dated molecular phylogenies (Muellner et al. 2008, Su and Saunders 2009, Nauheimer et al. 2012, Thomas et al. 2012, Grudinski et al. 2014, Hughes et al. 2015, Williams et al. 2017) and combined meta-analyses (van Welzen et al. 2011, De Bruyn et al. 2014, Crayn et al. 2015) have supplemented our knowledge of the geological and climatic history of the region. These studies have provided insights into where and when particular lineages diversified and revealed some remarkable cross-taxon biogeographic patterns (Lohman et al. 2011). Salient patterns emerging from a review of angiosperm research include the predominance of west to east dispersal patterns in the region (Su and Saunders 2009, Baker and Couvreur 2012, Richardson et al.

2012, Thomas et al. 2012, Grudinski et al. 2014, Richardson et al. 2014, Crayn et al. 2015); Borneo as an ancestral area and centre of diversity (Webb and Ree 2012, Van Welzen et al. 2014, Williams et al. 2017); high levels of floristic exchange on the Sunda shelf (Su and Saunders 2009, Thomas et al. 2012, Van Welzen et al. 2014, Williams et al. 2017) and increased diversification across the region from the late Miocene accelerating in the Plio-Pleistocene (Su and Saunders 2009, Nauheimer et al. 2012, Thomas et al. 2012, Grudinski et al. 2014, Richardson et al., 2014, Hughes et al. 2015). However, our current understanding of the biogeographic history of Malesia remains incomplete, primarily due to a lack of phylogenetic studies with detailed taxon sampling across the region (Richardson et al. 2012, Webb and Ree 2012). Our aim in this study is to test whether these key patterns are seen in one of the most emblematic and species-rich genera of the Malesian rainforest understorey, *Cyrtandra,* using the first well sampled phylogeny of the genus across the region.

Cyrtandra is the largest genus in the Gesneriaceae with over 800 species of herbs, shrubs and occasionally small trees and epiphytes (Atkins et al. 2013). Centres of diversity for the genus are Borneo (~200 spp.), the Philippines (~150 spp.), and New Guinea (~120 spp.) (Atkins et al., 2013). Approximately 175 species are also distributed across the Pacific Basin, with every major archipelago hosting numerous endemic species (Atkins et al., 2013). Its high diversity, large number of narrow endemic species, and wide distribution make it an ideal genus for examining biogeographic patterns (Atkins et al. 2001, Cronk et al. 2005, Clark et al. 2008, 2009, Johnson et al. 2017) and investigating the processes which underlie current patterns of biodiversity (Bramley et al. 2004a, Johnson et al. 2015, 2019). *Cyrtandra* is found predominantly in the rainforest, from sea level to 3000m (Burtt 2001a, Atkins et al. 2013). The genus is characterised by a combination of two fertile stamens or very rarely four or five (Gillett 1970, 1973) and an indehiscent fruit which varies from a tough-walled, green or brown capsule in the west (Fig. 4.1) to a fleshy berry which ripens white or occasionally orange in the east of its distribution, particularly in New Guinea and the Pacific (Clark et al. 2013, Johnson et al. 2017, Atkins et al. 2019). The flowers are often white but species with pink, red, yellow, green and orange flowers are also known (Fig. 4.2).

Fig 4.1: Range of fruit morphology in SE Asian and Pacific *Cyrtandra*. a *C. pendula* (Sumatra) SUBOE 2; b *C.* sp (Sumatra) SUBOE 6; c *C.* sp (Sumatra) SUBOE 9; d *C.* sp (New Guinea) Briggs MB838; e *C. pogonantha* (Samoa) Wood 16941 f *C. celebica* (Sulawesi) BAKK 12; g *C. polyneura* (Sulawesi) BAKK 18; h *C. pulleana* (New Guinea) Briggs MB845; I *C. richii* (Samoa) Wood 16935. Photos: a-c, f & g: Sadie Barber. e & i: Melissa Johnson. d & h: Marie Briggs.

Fig. 4.2: Range of flower morphology in SE Asian *Cyrtandra*. a *Cyrtandra rantemarioensis* (Sulawesi) RBGE living collections 20000622; b. *Cyrtandra luteiflora* (Sulawesi) RBGE living collections 20021194; c. *Cyrtandra purpureofucata* (Sulawesi) Thomas & Ardi 09-88; d. *Cyrtandra serratifolia* (Sulawesi) RBGE living collections 20021210; e. *Cyrtandra celebica* (Sulawesi) BAKK 15; f. *Cyrtandra mollis* (Sulawesi) BAKK 42; g. *Cyrtandra cleopatrae* (Palawan, Philippines) RBGE living collections 19981745; h. *Cyrtandra bungahijau* (Yapen Island, New Guinea) RBGE living collections 20090826; i. *Cyrtandra peltata* (Sumatra) RBGE living collection 20161282; j. *Cyrtandra vittata* (Yapen Island, New Guinea) RBGE living collection 20090734. Photos: a & b: Steve Scott. c: Wisnu Ardi. d & g: Hannah Atkins. e, f & i: Sadie Barber. j: Lynsey Wilson

Earlier phylogenetic studies of Southeast Asian *Cyrtandra* have focused on particular localities with dense sampling from a small number of locations (Atkins et al., 2001, Bramley et al., 2004a). Larger scale studies examining *Cyrtandra* diversification across the Pacific (Cronk et al. 2005, Clark et al. 2008, 2009, Johnson et al. 2017) have included a small number of taxa from key locations in Southeast Asia. Results of the Pacific studies suggest that the origin of the genus is within the Malesian region, and that founder events and speciation within islands were both important in the evolution of the genus (Johnson et al. 2017). Here we sample *Cyrtandra* taxa from key localities across Southeast Asia to construct a well-resolved phylogeny based on one nuclear and four chloroplast regions. Using this phylogenetic framework we estimate divergence times, ancestral ranges, colonisation patterns, and the importance of various biogeographic processes to gain insights into the evolutionary history of *Cyrtandra.* Additionally, we seek to determine if biogeographic patterns in this large and widely distributed genus align with some of the emerging themes in plant biogeography in the Malesian region, namely:

1. Diversification in the region from the late Miocene
2. West to east dispersal
3. Borneo as a major evolutionary hotspot
4. High levels of floristic exchange on the Sunda shelf

4.2 Material and Methods

4.2.1 Taxon sampling

We sampled a total of 192 accessions representing 128 *Cyrtandra* taxa (Appendix 4.1). We included samples that were representative of all the key regions in Southeast Asia, with as many of the islands included as possible (Fig. 4.3). Table 4.1 gives a summary of our sampling against current estimates of species numbers by island for the Southeast Asian region (Atkins et al. 2013). Six taxa from within the Didymocarpinae (the same subtribe as *Cyrtandra*) were selected as outgroups (*Aeschynanthus roseoflorus, A. buxifolius, Agalmyla chalmersii, Didymocarpus antirrhinoides* and *Loxostigma griffithii*). These allowed unequivocal rooting of the tree but were also closely related enough to allow unambiguous alignment of the sequence data. Outgroups were also selected to reflect those included in recent molecular dating analyses (Johnson et al. 2017, Ranasinghe 2017) to facilitate dating of the nodes using secondary calibration points. We applied names to as many of the samples as possible but much taxonomic work is still required and many of the samples represent undescribed diversity. We included a number of taxa named only to genus level (13 samples

representing 13 taxa), section level (2 samples representing 2 taxa), or with some degree of affinity to a known species (as aff. or cf.) (21 samples representing 16 taxa).

Geographic region (Southeast Asia only)	Total number of species (following Atkins et al. 2013)	Number of species sampled	% sampled (based on maximum numbers where ranges given in Atkins et al. 2013)
Thailand	6	2	33
Peninsular Malaysia	9	5	56
Sumatra	40-44	27	61
Java	19-32	11	34
Lesser Sunda Islands	3	1	33
Borneo	181-200	26	13
Taiwan and Japan	2	2	100
Philippines	105-150	17	11
Sulawesi	22-40	26	65
Moluccas	3	0	0
Australia	1	1	100
New Guinea	107-120	10	8

Table 4.1. Current estimates of species numbers in *Cyrtandra* by area across Malesia, the number of species included in the present study, and the percentage of the total that this represents.

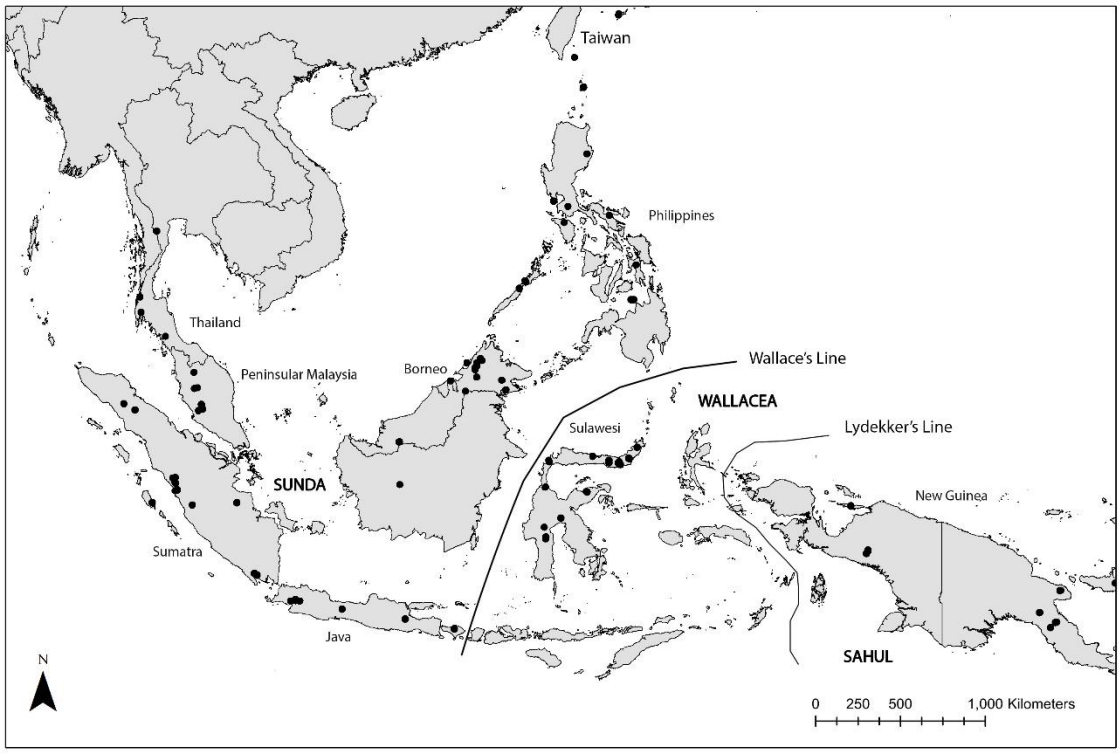

Fig. 4.3. Map of southeast Asia showing collection locations of *Cyrtandra* samples included in the present study.

4.2.2 Molecular methods

Total genomic DNA was extracted from fresh leaf material or silica dried material using a modified CTAB procedure (Doyle & Doyle, 1987) or using the Qiaxtractor (Qiagen, Hilden). One nuclear (ITS) and four chloroplast regions (*mat*K, *trn*L-F, *psb*A-*trn*H and *rpl*32-*trn*L) were sampled. PCR was carried out with Biotaq DNA polymerase (Bioline, London) and with CES PCR enhancer (Ralser et al., 2006) with the following chemical concentrations (10× buffer 1µl, 20mM dNTP 1 µl, 50 mM $MgCl_2$ 0.3 µl, forward and reverse primers 0.4 µl each, CES 2 µl, Biotaq 0.2 µl, DNA 1 -2 µl anddH_2O added to make up 10 µl). PCR amplifications were carried out under the following conditions: ITS and *mat*K: 94°C for 4 min, 35 cycles of 94°C for 1 min, 55°C for 1 min, 72°C for 1.5 min, followed by 72°C for 10 min; *trn*L-F: 94°C for 4 min, 35 cycles of 94°C for 30 seconds, 57°C for 30 seconds, 72°C for 1 min, followed by 72°C for 10 min; *psb*A-*trn*H and *rpl*32-*trn*L: 94°C for 4 min, 35 cycles of 94°C for 1 min, 52°C for 1 min, 72°C for 1.5 min, followed by 72°C for 10 min. The primers used in this study are listed in Table 4.2. All PCR amplifications were carried out on a Bio-Rad Tetrad DNA Engine (Bio-Rad, Hercules, CA). The PCR products were visualised under UV light after electrophoretic separation on a 1% agarose gel stained with SYBR Safe gel stain (Invitrogen, Carlsbad, CA). PCR products were subsequently purified using ExoSAP-IT (Thermo Fisher Scientific, Waltham, MA) following the manufacturer's protocol. PCR products were sequenced using the BigDye™ Terminator v 3.1 Cycle Sequencing Kit (Applied Biosystems™, Foster City, CA) following the manufacturer's protocol, with the same primers used for PCR amplification. Sequencing was carried out by Edinburgh Genomics at the University of Edinburgh. The resulting electropherograms were combined and edited in Sequencher v 5.1 (Gene Codes Corporation, Ann Arbor, MI) and a matrix assembled, aligned and manually adjusted in Bioedit v 7.1.11 (Hall, 1999). Chloroplast sequence data (*mat*K, *trn*L-F, *psb*A-*trn*H and *rpl*32-*trn*L) from two of the outgroup collections, *Agalmyla chalmersii* and *Didymocarpus antirrhinoides,* was gifted to the project by Prof Gao Lianming, Kunming Institute of Botany, Chinese Academy of Sciences, Yunnan, China.

Region	Name	Direction	Primer sequences	References
ITS	ITS_5P	Forward	GGA AGG AGA AGT CGT AAC AAG	Möller & Cronk 1997
ITS	ITS_8P	Reverse	CAC GCT TCT CCA GAC TAC A	Möller & Cronk 1997
*trn*LF	trnLcG	Forward	GTG AAG ACT TCT AAA TTC AGA GAA AC	Nishii et al., 2019
*trn*LF	trnLf	Reverse	ATT TGA ACT GGT GAC ACG AG	Taberlet et al. 1991
*psb*A-*trn*H	psbAf	Forward	GTT ATG CAT GAA CGT AAT GCT C	Sang et al. 1997
*psb*A-*trn*H	trnHr	Reverse	CGC GCA TGG TGG ATT CAC AAA TC	Sang et al. 1997
*rpl*32-*trn*L	rpl32-F	Forward	CAG TTC CAA AAA AAC GTA CTT C	Shaw et al. 2007
*rpl*32-*trn*L	$trnL^{(UAG)}$	Reverse	CTG CTT CCT AAG AGC AGC GT	Shaw et al. 2007
*mat*K	matK.206F	Forward	CCG GGT TAT GAC AAT AAA TCC AGT	Luna et al., 2019
*mat*K	matK.946R	Reverse	ATA AAT CCT TCT TGG ATG AAA CCA C	Luna et al., 2019
*mat*K	matK.cy2F	Forward	TGG CAA TGG CAT TTT TCG CT	Nishii et al., 2019
*mat*K	matK.1734R	Reverse	CCG TGC TTG CAT TTT TCA TTG C	Luna et al., 2019

Table 4.2: Details of primers used for PCR and sequencing of the five gene regions for *Cyrtandra*.

4.2.3 Phylogenetic analyses

Maximum Parsiomony (MP) analyses were initially conducted on individual regions to visually assess congruence, with areas of conflict determined by examining the placement of individual taxa on each gene tree. Relationships were considered incongruent if the placement of taxa varied among the individual gene trees and exhibited MP-BS values > 80%. MP analyses were carried out using PAUP v 4.0a163 (Swofford, 2002) on unweighted and unordered characters. Alignment gaps were treated as missing data. A heuristic search was carried out using stepwise random addition of 10,000 replicates, with TBR and Multrees on. Statistical branch support was obtained from 10,000 heuristic bootstrap replicates each starting with a random addition tree, optimised with TBR on and Multrees off. For Bayesian Inference and Maximum Likelihood analyses, the data were divided into seven partitions (ITS spacers, 5.8S gene, *psbA-trnH*, *rpl*32-*trn*L, *trn*L-F, *matK* coding region, *matK* intron region), and analysed under the best-fit model of nucleotide evolution for each genic region selected using the AIC criterion as implemented in MrModeltest v 2.4 (Nylander, 2004) (GTR+G for ITS spacers, *trn*L-F, *psbA-trnH* and *matK* intron region, GTR+I+G for *rpl*32-*trn*L and *matK* coding region and SYM+I for the ITS 5.8S gene). Bayesian inference (BI) phylogenetic analyses were carried out using Mr Bayes v 3.2.6 (Ronquist et al., 2012) on the partitioned dataset. Two runs with four chains each were implemented, run for 10,000,000 generations with a tree sampled every 1000th generation. The first 10% of sampled trees were discarded as burn-in and the remainder

summarised as a maximum clade credibility tree and posterior probabilities (PP) extracted. Maximum Likelihood (ML) analyses were conducted with RAxML v 8 (Stamatakis, 2014) via the CIPRES Gateway (Miller et al., 2010). The search for the optimal ML tree was performed with the 'Let RAxML halt bootstrapping automatically' parameter selected. For the ML and BI analyses, tree topology and node support were examined in FigTree v. 1.4.3 (Rambaut, 2007).

4.2.4 Divergence time estimates

A time-calibrated phylogeny was constructed on the partitioned five-gene dataset using an uncorrelated relaxed lognormal clock in the program BEAST v. 1.10.1 (Drummond et al. 2012, Rambaut et al. 2018). Secondary age calibrations were necessary as there are no unambiguous fossils in the Gesneriaceae family (Wiehler 1983, Clark et al. 2008). Five calibration points were taken from the family-wide phylogeny in Ranasinghe (2017) (Table 4.3) and were assigned a lognormal prior following Ho & Phillips (2009) and Schenk (2016). Sensitivity analyses using a normal prior were also run and the results were not significantly changed. Five separate runs were carried out beginning with a random tree and run for 100 million generations under a Yule model of speciation, sampled every 1000 generations. Following Condamine et al. (2015) sensitivity analyses using the Birth-Death tree prior were also run and the results were not significantly changed by choice of tree prior. The results from the analysis with the Yule model are presented here. Plots of the logged parameters for each run were visualised using Tracer v. 1.7.1 (Drummond and Rambaut 2007) to confirm convergence between runs by examining log likelihood plots and ensuring that Effective Sample Size (ESS) values were above 200. The trees from each run were combined in Logcombiner v 1.10.1 (Drummond et al. 2012) and support values and tree statistics were summarised onto a single maximum clade credibility (MCC) tree using the programme TreeAnnotator v. 1.10.1 (Drummond et al. 2012), visualised in FigTree v. 1.4.3 (Rambaut 2007).

Calibration point	Node	Node Age (Ma)	Prior distribution	Standard deviation
1	Internal *Cyrtandra* node	6.42	Ln	2.0 (2.5, 10.97)
2	*Loxostigma* and *Cyrtandra* crown	18.03	Ln	2.0 (14.18, 21.85)
3	*Aeschynanthus* and *Loxostigma/ Cyrtandra* crown	18.79	Ln	2.0 (14.89, 22.71)
4	*Billolivia* (and *Aeschynanthus/Loxostigma/ Cyrtandra* crown	20.15	Ln	2.0 (16.18, 24.28
5	*Agalmyla* (and *Billolivia/ Aeschynanthus/ Loxostigma/ Cyrtandra* crown)	20.99	Ln	2.0 (17.04, 25.14

Table 4.3. Details of the five secondary calibration points (node age, standard deviation and prior distribution) from Ranasinghe (2017) used to generate the dated phylogeny of *Cyrtandra* in BEAST.

4.2.5 Ancestral range estimation

The R package BioGeoBEARS (BioGeography with Bayesian Evolutionary Analysis in R Scripts) (Matzke 2013, 2014) was used to estimate ancestral ranges for *Cyrtandra* under three historical biogeography methods: DEC (Dispersal-Extinction-Cladogenesis (Ree and Smith, 2008)), DIVA (Dispersal-Vicariance Analysis (Ronquist 1997)) and BayArea (Bayesian inference of historical biogeography for discrete areas (Landis et al. 2013)) models. Descriptions of each of these models and how BioGeoBEARS replicates their key assumptions are given in Matzke (2013). To allow for model comparison, all of the models were implemented in a maximum likelihood framework. As *Cyrtandra* is distributed across a system of islands and shows high levels of narrow endemism, founder event speciation was likely to be a highly relevant biogeographic process (Cowie and Holland 2006, Matzke 2013, Roalson & Roberts, 2016, Johnson et al. 2017) so we also explored the influence of founder event speciation in the analysis by including '+J' versions of the models. Due to concerns about the statistical methods in the package, both in terms of how the best fit model is selected and how the +J parameter operates (Ree and Sanmartín 2018) results from all of the six models will be discussed. Given that sampling density can also impact the results, a summary of our sampling rates against current species estimates is presented in Table 4.1.

The MCC tree was pruned to include only a single representative of each species except for those that have multi-island distributions and were not monophyletic, such as *C. pendula*. In these cases we included one representative from each area (following Johnson et al. 2017, 2019). For monophyletic species with multi-island distributions, such as *C. umbellifera* from Taiwan and the Philippines and *C. sandei* from Java and Sumatra, only one sample was included and these were coded as present in each respective area in the analysis. Each taxon was assigned a distribution using 13 geographic regions based on a combination of geological information (Hall 2002, 2012), previous biogeographical studies (Atkins et al. 2001, van Welzen et al. 2011, Hughes et al. 2015) and current knowledge of species distributions and relationships in *Cyrtandra* (Atkins & Cronk 2001, Bramley & Cronk 2003, Johnson et al. 2017, Kartonegoro et al. 2018). The 13 regions used were: Hawaii, Marquesas and Society Islands, Japan and Taiwan, Australia, Thailand, Peninsular Malaysia, Sumatra, Borneo, Sulawesi, New Guinea, Solomon Islands, Java and the Lesser Sunda Islands, and the Philippines (See map included in Figure 4.4, 4.5).

The outgroup taxa were removed so as not to influence the root ancestral area. We set the maximum number of areas to two, as *Cyrtandra* is characterised by high levels of narrow endemism and only *C. pendula* is currently recognised as having a range size greater than two areas. The six models (DEC, DIVA-like, BayArea-like, and the '+J' variations of each) were compared for statistical fit using the Akaike Information Criterion (AIC) and a Likelihood Ratio Test (LRT).

Lastly, we used BioGeoBEARS to perform a Biogeographic Stochastic Mapping (BSM) analysis (Matzke 2016, Dupin et al. 2017). This generates simulated histories based on a given biogeographical model, the phylogeny, observed range data and the calculated ancestral state probabilities at each node averaged over many realisations. The biogeographical events that are possible include within-area speciation, vicariance and dispersal events (range expansions and founder events). Event frequencies were estimated by taking the mean of event counts from 100 BSMs. We ran the BSM exercise on all of the models, to evaluate the impact that the choice of model has on the event counts.

4.3 Results

4.3.1 Phylogenetic relationships

In total, 940 new sequences were generated for this study and our final data matrix contained five gene regions and 5438 aligned base positions. Tree topologies of independent MP analyses of the ITS, *trn*L-f, *psb*A-*trn*H, *rpl*32 and *mat*K regions were congruent although there was far greater resolution in the ITS dataset than in any of the others individually. The tree based on the

concatenated five-gene dataset (Fig. 4.4,4.5) largely followed the topology of the ITS tree with increased support for the relationships between the major clades. There were no incongruences with greater than 80% MP bootstrap support. ML, MP and BI analyses of the combined dataset resulted in trees with congruent topologies.

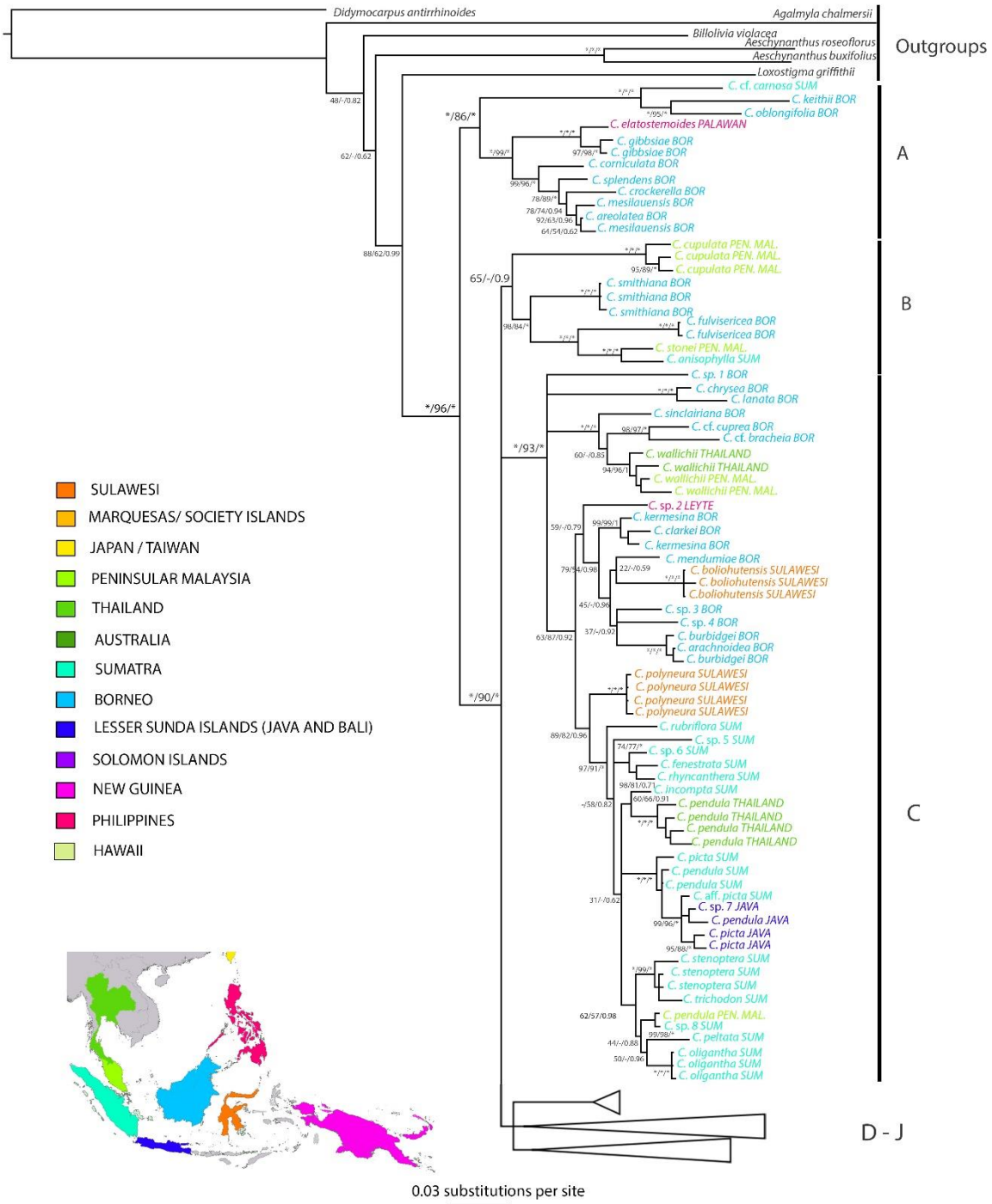

Fig. 4.4**.** Bayesian inference tree of *Cyrtandra* based on the combined ITS, *psb*A-*trn*H, *rpl*32-*trn*L, *trn*L-F, and *mat*K regions and highlighting the three most basal clades (A, B and C). Node support is indicated as Maximum likelihood Bootstrap support (ML-BS), Maximum Parsimony Bootstrap support (MP-BS) and Bayesian Posterior Probabilities (BI-PP). Maximum values (100% BS or 1.0 PP) are indicated by *. No support (< 50% BS or 0.50 PP) is indicated by -. Species names are colour-coded by geographic region. Pacific islands not shown on map.

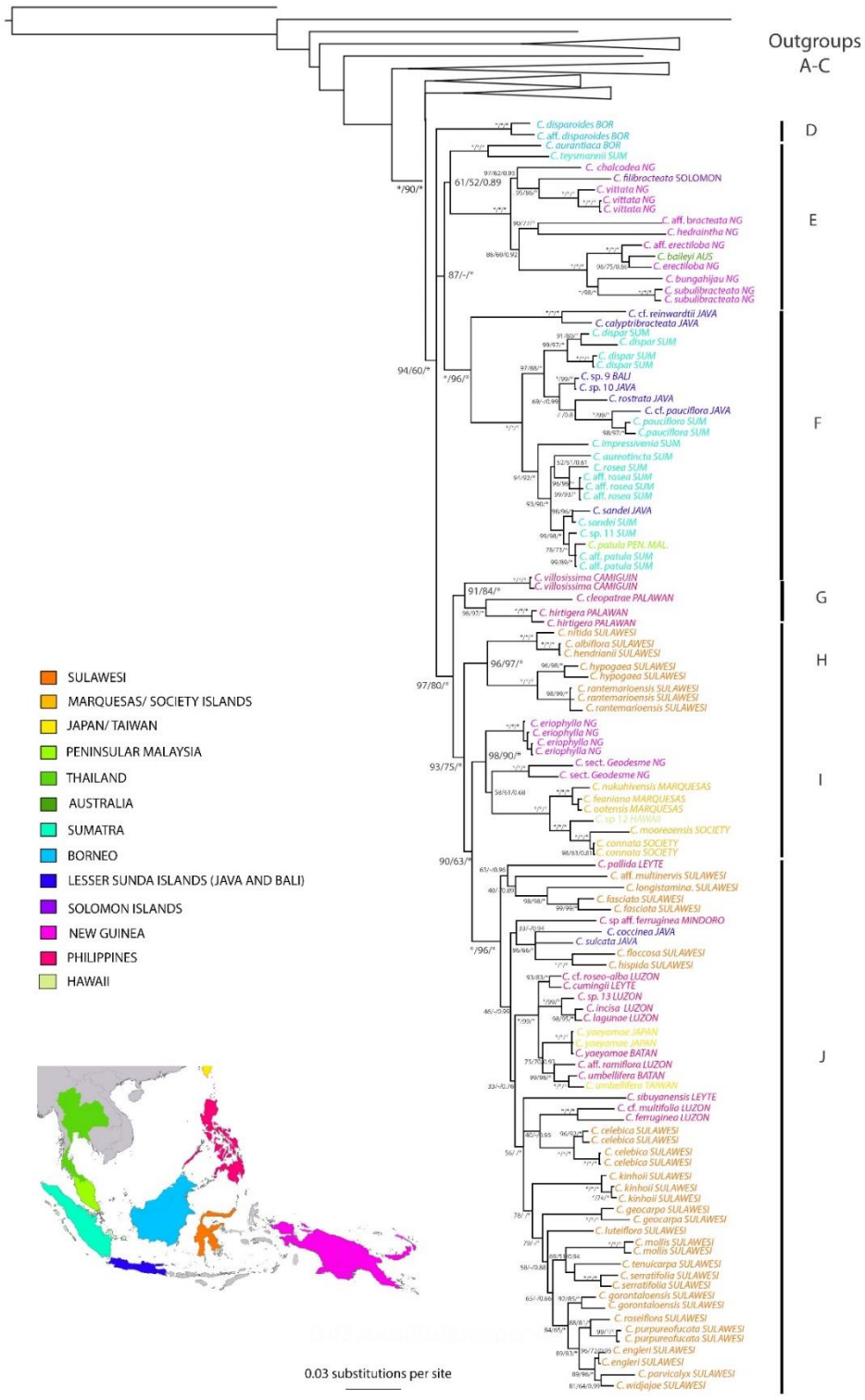

Fig. 4.5**.** Bayesian inference tree of *Cyrtandra* based on the combined ITS, *psb*A-*trn*H, *rpl*32-*trn*L, *trn*L-F, and *mat*K regions, and highlighting clades D-J. Node support is indicated as Maximum Likelihood Bootstrap Support (ML-BS), Maximum Parsimony Bootstrap Support (MP-BS) and Bayesian Posterior Probabilities (BI-PP). Maximum values (100% BS or 1.0 PP) are indicated by *. No support (< 50% BS or 0.50 PP) is ndicated by -. Species names are colour-coded by geographic region. Pacific islands not shown on map.

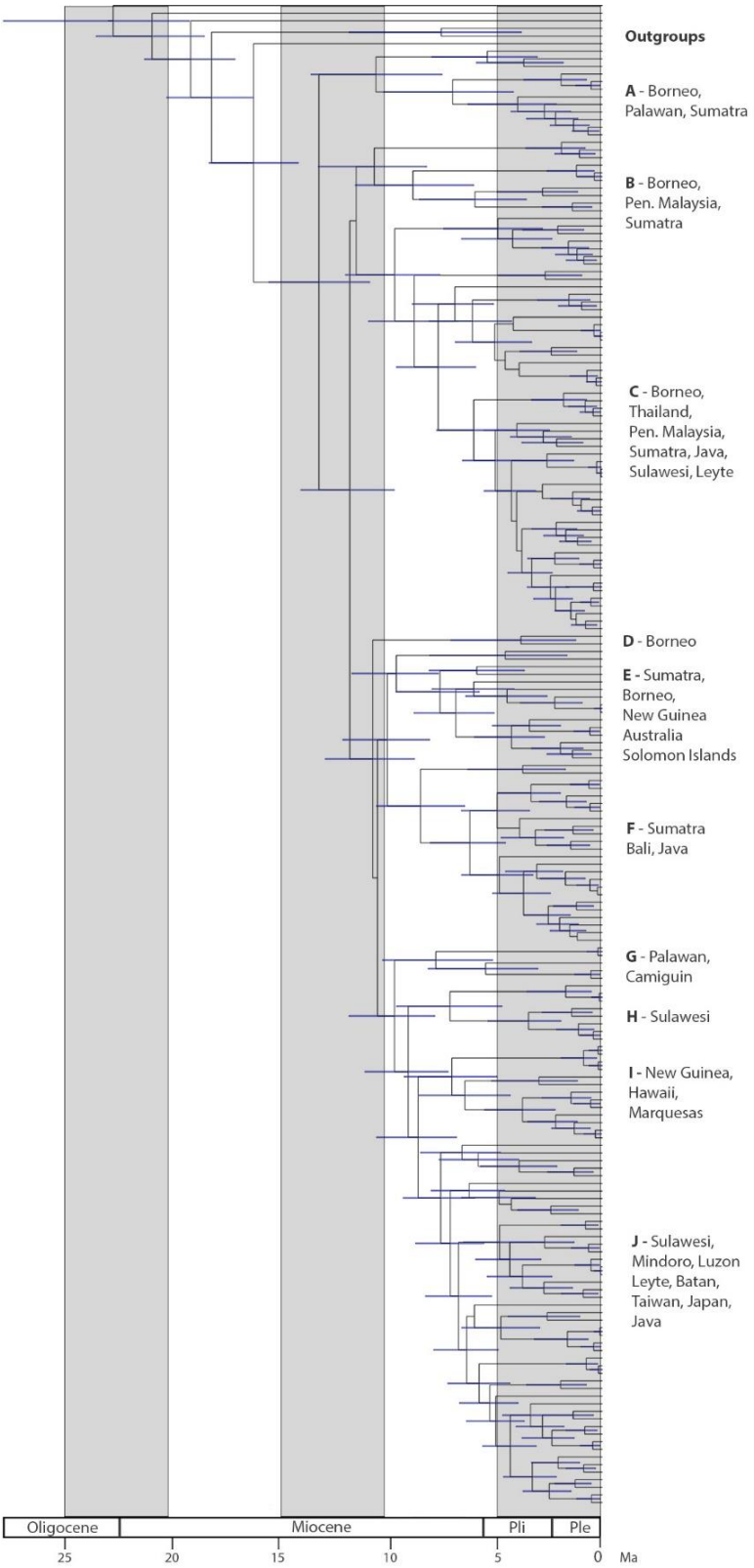

Fig. 4.6. Maximum clade credibility tree of *Cyrtandra* based on a BEAST analysis of the combined ITS, *psb*A-*trn*H, *rpl*32-*trn*L, *trn*L-F, and *mat*K regions. Mean divergence time estimates are shown as millions of years ago (Ma) with the blue boxes showing the 95% highest posterior density (HPD). Pliocene is abbreviated to Pli and Pleistocene to Ple in the Time Scale below the tree.

4.3.2 Divergence time estimates

In this study, divergence time estimates suggest that the genus *Cyrtandra* split from its closest relative, *Loxostigma,* c. 16 Ma (14.18-18.34, 95% HPD) during the early Miocene (Fig. 4.6). The crown age of *Cyrtandra* is estimated to be 13 Ma (10.84-15.56, 95% HPD). Summaries of estimated dates are shown in Table 4.4. These dates are similar to those reported for *Cyrtandra* in Roalson and Roberts (2016) and Johnson et al. (2017) and significantly younger than those reported in Clark et al. (2008, 2009) (Table 4.4). These last, much earlier, dates were based strictly on the geological ages of islands, an approach which has been shown to be problematic (Renner, 2005, Heads 2011). Using mean ages, 109 of the 128 taxa included in the analysis split from their sister lineage in the last 5 myr (method following Madriñán et al. 2013, Richardson et al. 2014).

Node	Present study	Johnson et al. 2017	Roalson & Roberts 2016
Cyrtandra stem	16.3 (14.28-18.43)	25.27 (16.9-35.02)	30.45 (14.79-37.54)
Cyrtandra crown	13.38 (11.05-15.79)	17.29 (12.54-22.15)	11.08 (3.25-21.78)

Table 4.4. Estimated ages (Ma) of major nodes (crown and stem age of *Cyrtandra*) in the present study using BEAST, and comparable nodes in earlier studies. Ranges in parentheses represent the 95% highest posterior density (HPD).

4.3.3 Ancestral range estimation

Significant improvement in the likelihood of the three standard models (DEC, DIVA-like and BayArea-like) was seen when the founder event parameter (+J) was added (Table 4.5). Of the six models evaluated, the best fit model was BayArea-like +J.

Model	LnL	AIC	AIC_wt	# parameters	d	e	j
DEC	-258.8	521.7	1.80E-21	2	0.0055	0.014	0
DEC+J	-216	438	0.0027	3	0.0012	1.00E-12	0.013
DIVALIKE	-252.4	508.7	1.20E-18	2	0.0058	1.00E-12	0
DIVALIKE+J	-218.3	442.6	0.0003	3	0.0014	1.00E-12	0.013
BAYAREALIKE	-280.4	564.8	8.00E-31	2	0.0059	0.092	0
BAYAREALIKE+J	**-210.1**	**426.2**	**1**	**3**	**0.0005**	**0.0043**	**0.013**

LnL = Log Likelihood, AIC = Akaike Information Criterion, AIC wt = weighted AIC

Table 4.5. Results of biogeographical model testing in BioGeoBEARS for *Cyrtandra*. Model parameters include anagenetic dispersal (d), extinction (e) and jump dispersal or founder events (j). The best fit model of BayAreaLike+J is highlighted in bold.

Under all six models analysed, the island of Borneo was recovered as the most likely ancestral area for *Cyrtandra* (Fig. 4.7). Borneo is also the most likely ancestral area for all of the early diverging clades, clades A-F, which are predominantly of Sunda shelf origin but also contain taxa from New Guinea and Australia. The Philippines is the most likely ancestral area for the large, predominantly Wallacean and eastern, clade (comprising smaller clades G-J) with taxa from Sulawesi, the Philippines, the Pacific and Japan and Taiwan (Fig.4.7).

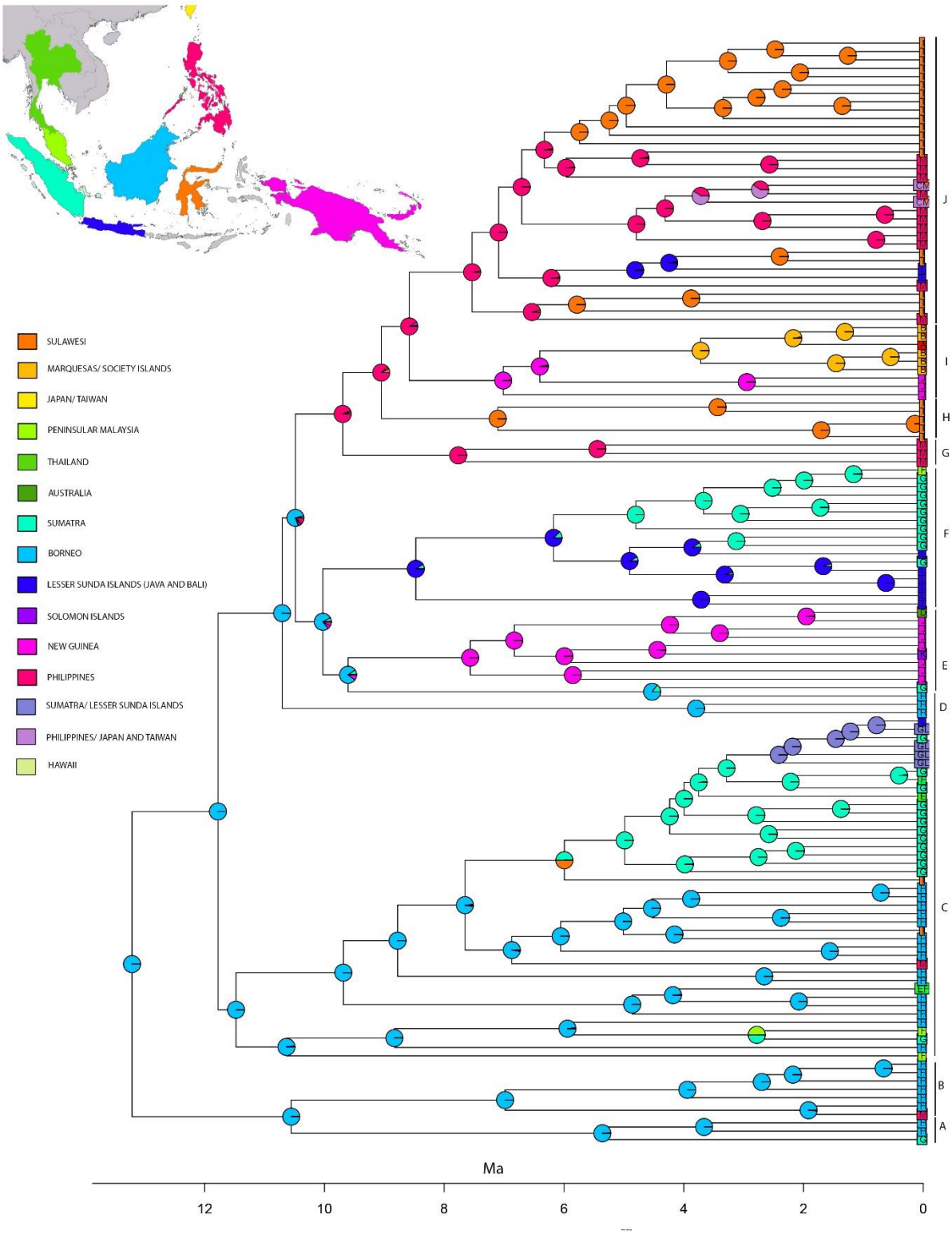

Fig. 4.7**.** Ancestral range estimation for *Cyrtandra* based on the ultrametric tree produced in BEAST, and the best model determined by BioGeoBEARS (BayArea-like +J). Areas are colour-coded for the 13 geographic regions used in the analysis. Pacific islands not shown on map. Pie graphs at each node indicate the probability of a given area (or combined areas).

4.3.4 Biogeographic stochastic mapping

Under the best fit model, Borneo is resolved as a major source area with ~33% (11.5 events) of all dispersal events originating here (Fig. 4.8, Table 4.6). Dispersal from Borneo was most frequently to Sumatra (3.0 events) and the Philippines (2.7 events) followed by Peninsular Malaysia (2.0 events) and Sulawesi (1.5 events). In contrast, Borneo was the recipient of only 0.8% of dispersals from all other areas and no event counts from any single area above 0.1. The Philippines was the second largest source area with 21% of dispersal events originating here. The majority of dispersal events from the Philippines were to the island of Sulawesi (3.9 events) but there were also dispersals from the Philippines north to Taiwan and Japan (1.5 events) and east to New Guinea (0.9 events). The greatest source of dispersals into the Philippines was Borneo (2.7 events). Relatively high levels of dispersal were also recovered between Java, Sumatra and Peninsular Malaysia (2.5 events from Sumatra to Peninsular Malaysia, 3.0 events from Java to Sumatra and 1.2 events from Sumatra to Java). In marked contrast to Borneo, Sulawesi emerged as an island of high immigration (receiving 20% of all dispersals) and low emigration with only 2% of dispersals originating here. New Guinea is resolved as the most likely source of dispersals to the Marquesas (0.9 events), Australia (1.0 event) and the Solomon Islands (1.0 event). The stochastic mapping exercise is more impacted by the choice of model than the ancestral range estimation as the six models rely on different biogeographic processes. In terms of dispersal patterns and potential routes through the region, however, Borneo is always in the top three sources of dispersal in all of the models along with the Philippines and Sumatra. Sulawesi is always interpreted as being a poor source of dispersals under all models. The Philippines is the most important source of dispersals north to Taiwan and Japan under all models, the highest source of dispersals south to Sulawesi in all but the two worst fit models where it is the second highest after Borneo; and the highest source of dispersals east to New Guinea in all but the two worst fit models where Sumatra, Sulawesi or Borneo are interpreted as the most important source. New Guinea is the most likely source of dispersals to Australia, the Marquesas/ Society Islands and the Solomon Islands under all models.

	TO	A	B	C	D	E	F	G	H	I	J	K	L	M	TOTALS	As %
FROM		Hawaii	Marquesa/SI	Japan/Taiwan	Australia	Thailand	P. Malaysia	Sumatra	Borneo	Sulawesi	New Guinea	Solomon	Java/Bal	Philippines		
A	Hawaii	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0.1	0.3
B	Marquesas/ Society Is	1.0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	2.8
C	Japan/ Taiwan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D	Australia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E	Thailand	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0.5	1.4
F	Pen. Malaysia	0	0	0	0	0.5	0	0.5	0	0	0	0	0	0	1.0	2.8
G	Sumatra	0	0	0	0	1.0	2.5	0	0.1	0.5	0.1	0	1.2	0	5.4	15.3
H	Borneo	0	0	0	0	0.5	2.0	3.0	0	1.5	0.9	0	0.9	2.7	11.5	32.7
I	Sulawesi	0	0	0	0	0	0	0.5	0	0	0	0	0	0.2	0.7	2.0
J	New Guinea	0	0.9	0	1	0	0	0	0.1	0.1	0	1	0.1	0.2	3.4	9.7
K	Solomon Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L	Java and Bali	0	0	0	0	0	0	3.0	0	1.0	0.1	0	0	0.1	4.2	11.9
M	Philippines	0	0	1.5	0	0	0	0	0.1	3.9	0.9	0	1	0	7.4	21.0
TOTALS		1	1	1.5	1	2	5	7	0.3	7	2	1	3.2	3.3	35.3	
As %		2.8	2.8	4.2	2.8	5.7	14	20	0.8	20	5.7	2.8	9.1	9.3		100

Table 4.6. Summary of all dispersal counts for *Cyrtandra* averaged across 100 BSMs in BioGeoBEARS. Mapping was performed using parameters from the best-fit model of BayArea-like+J. Colour temperature indicates the frequency of events, with warmer colours indicating more common events (Red = >2.9, Orange = 2.0-2.9, Yellow = 0.9-1.9, Green = < 0.9). The ancestral states (i.e. where the lineage dispersed from) are given in the row, and the descendant states (where the lineage dispersed to) are given in the column.

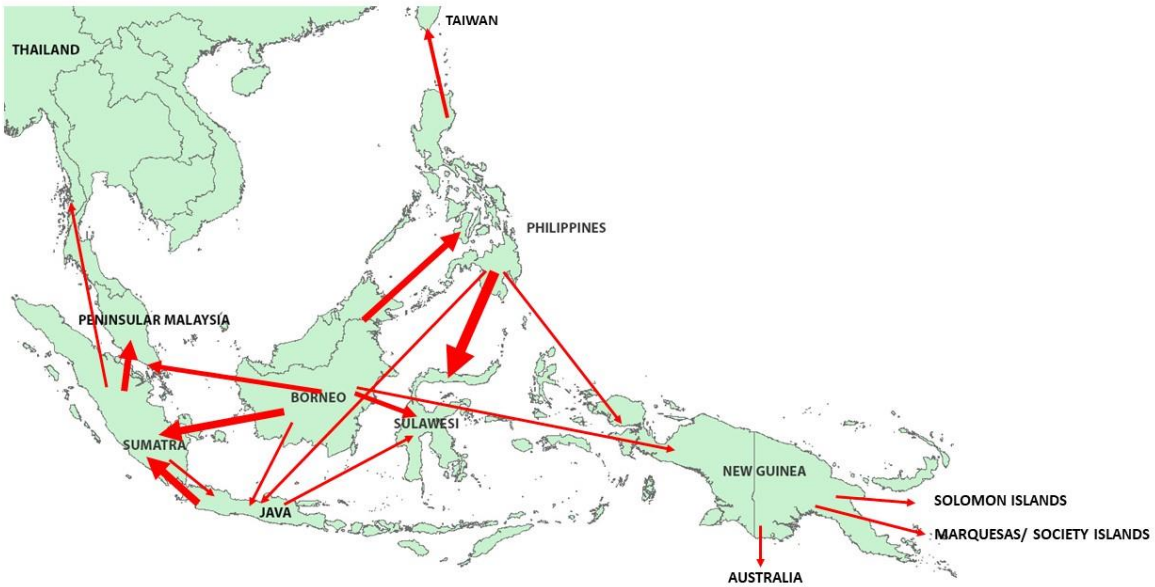

Fig. 4.8. Summary of dispersal events in *Cyrtandra* estimated using a Biogeographic Stochastic Mapping (BSM) analysis in BioGeoBEARS based on the best fit model of BayArea+J (full results given in Table 4.6). The weight of each line indicates the number of predicted dispersal events (both founder and range expansion). All event counts of 0.9 and above are included.

4.4 Discussion

4.4.1 Diversification across the region from the late Miocene

The origin and early diversification of *Cyrtandra* in the region dates to the mid Miocene (crown age 13 mya) and most of the current diversity in Southeast Asia is the result of speciation in the last 5 my (Fig. 4.6) with 85% occurring in this period. This pattern of diversification starting in the mid Miocene with most speciation occuring in the last 5 my, is extensively reported in studies of Southeast Asian taxa such as *Begonia* (Thomas et al., 2012) and *Aglaia* (Grudinski et al. 2014) and is highlighted by de Bruyn et al. (2014) in their meta-analysis of regionial biodiversity. The presence of land in the centre of the region for the first time approximately 23 mya as the Sunda and Sahul shelves moved closer (Hall, 2002, Hall, 2012a, b); subsequent rapid orogenesis in key islands such as Sulawesi and New Guinea (Hall, 2002, Hall, 2012a, b); and the cyclic vicariance caused by the frequent habitat fragmentations and amalgamations due to the climate and sea-level fluctuations of the Pleistocene (Voris, 2000, Woodruff, 2010, Cannon et al., 2012, Morley, 2012) appear to be likely drivers for the increase in diversification seen during this period (Thomas et al., 2012, Richardson et al., 2014).

Using a simple diversification rate analysis based on a pure-birth model of diversification with a constant rate and no extinction (Magallon & Sanderson, 2001, Madriñán et al., 2013), the mean diversification rate for *Cyrtandra* in Southeast Asia is 0.49 speciation events per million years which is significantly higher than the rate of 0.089 events/my calculated by Magallon & Sanderson (2001) for angiosperms as a whole. The rates of Southeast Asian *Cyrtandra* diversification are comparable to that of the ecologically similar mega-diverse genus *Begonia* in the Neotropics (0.5 events/my), and in Asia (0.61 events/my) (Moonlight et al., 2015) but slower than in the Hawaiian lineages of *Cyrtandra* in which diversification rates as high as 3.5 events/my are reported (Johnson et al., 2019). Given the prevalence of hybridisation in the evolution of young, species-rich tropical groups such as *Begonia* (Hughes et al., 2018) and the fact that it has been recorded elsewhere in *Cyrtandra,* principally in Hawaii (Pillon et al., 2013, Johnson et al., 2015, 2019) but also more generally in the recent radiation of the genus in the Pacific (Johnson et al., 2017), it was notable that there was no incongruence between the nuclear and chloroplast datasets in this large Malesian sample and no detectable evidence of hybridisation. A recent study of reproductive isolation in four species of Hawaiian *Cyrtandra* showed that boundaries between sympatric *Cyrtandra* species are maintained predominantly through postzygotic barriers (Johnson et al., 2015). Similar studies in Southeast Asia would be useful to determine if postzygotic barriers are important in the maintenance of species boundaries in this region or whether pre-zygotic barriers have a greater role in Southeast Asia where floral divergence amongst sympatric populations is markedly greater than in the Hawaiian

archipelago or whether there are fewer species growing in sympatry in southeast Asia compared to the Pacific.

4.4.2 West to east dispersal

Cyrtandra is another example of the increasingly well-documented movement of taxa from the west to east of Southeast Asia, particularly in rainforest lineages (Su & Saunders, 2009, Richardson et al., 2012, Thomas et al. 2012, Grudinski et al. 2014, Crayn et al. 2015). There are examples of dispersal in the opposite direction such as in Proteaceae (Barker et al., 2007) and Myrtaceae (Sytsma et al., 2004), but there is a distinct asymmetry (Richardson et al., 2012, Crayn et al., 2015). The west to east dispersal appears to have been particularly prevalent from the mid Miocene onwards as warmer and wetter conditions prevailed, rainforest expanded and extant land emerged east of Wallace's Line (Richardson et al., 2012, Grudinski et al., 2014, Crayn et al., 2015). Richardson et al. (2012) observed that this asymmetry could not be explained in terms of prevailing ocean current or wind direction as they are predominantly from east to west and instead was most likely explained by (i) the discrepancy in size of source areas, with the Sunda shelf providing a significantly more extensive area of rainforest for most of the past 50 mya relative to the Sahul shelf and therefore more available lineages; (ii) the Sunda shelf having a more stable geological history and consequently a more established flora and fewer available niches; (iii) the migrating taxa showing high levels of phylogenetic niche conservatism such that the wet forest adapted lineages coming from the Sunda region have a greater ability to establish on the emerging land in the east relative to taxa coming from, for example, Australia where the ancestral niche was from a more xeric environment.

The earliest example of a Sahul-Sunda disjunction (evidence of long distance dispersal from one shelf to the other) in *Cyrtandra* is between clade D and E at 9.6 mya (7.64-11.68 mya, 95% HPD) with the dispersal, being from Sunda to Sahul. This is comfortably within the time-frame of Sahul-Sunda disjunction events compiled by Crayn et al. (2015). Many of the *Cyrtandra* taxa east of Wallace's Line are characterised by fleshy berries as opposed to the predominantly dry indehiscent capsules of the Sunda shelf taxa (Fig. 4.1) (Burtt, 2001a, Johnson et al., 2017). It has been speculated that this change in fruit morphology is associated with a transition in dispersal mode from possible small mammal dispersal to bird dispersal (Gillett, 1967, Burtt, 2001a). A zoochorous dispersal mode is presented by Crayn et al. (2015) as being the most prevalent for Sunda-Sahul dispersals with 90% of ancestral species possessing zoochorous propagules, and it seems likely that the transition to fleshier berries has facilitated dispersal of *Cyrtandra* across the region. As the majority of species in the Sahul clade (Clade E), including *C. vittata* and *C. bungahijau* from New Guinea, *C. baileyi* from

Australia, and *C. subulibractea* from the Solomon Islands, have fleshy fruits (Gillett, 1975, Atkins et al., 2019), it seems likely that it is the ancestral state for this clade.

West to east dispersal patterns have also been well documented from New Guinea into the eastern Pacific (Keast, 1996). *Cyrtandra* is notable in being the only Malesian Gesneriaceae genus with a distribution that extends significantly into the Pacific (Hilliard & Burtt, 2002). The large Malesian genera *Aeschynanthus* and *Agalmlya* have wind-dispersed seeds and, despite being highly diverse in New Guinea do not extend beyond the Solomon Islands and the Louisade Archipelago (Hilliard & Burtt, 2002) respectively. Johnson et al. (2017) reported strong asymmetry in the direction of founder events in their study of *Cyrtandra* in the Pacific with the majority of dispersals occurring from a west to east direction which they also postulated was likely to be the result of bird dispersal, a mode identified by Carlquist (1996) as the most common plant dispersal syndrome for establishment into the Pacific. Johnson et al. (2017) also identified three dispersal events from New Guinea into the Pacific. Our sampling focus differed from this study but had four samples from New Guinea in common and we also identified three dispersal events from New Guinea: one to Australia, one to the Solomon Islands and one to the Marquesas. The routes to Australia and the Solomon Islands were reported by Johnson et al. (2017) and were suggested by Gillett (1975) based on his extensive knowledge of the *Cyrtandra* of New Guinea and the Pacific. He reported strong morphological affinities of the *Cyrtandra* of the Bismarck Archipelago and Solomon Islands and an attenuation of diversity as the number of New Guinea lineages reduced with distance from the island (Gillett, 1975). The third, and longest dispersal in this study, is to the Marquesas and originates in a completely separate clade of New Guinea samples to the other Pacific dispersals (Clade I). This clade containis samples of *C. eriophylla* and undescribed taxa from Section *Geodesme*, from Mt Jaya in Indonesian New Guinea in the south-east of the island. These samples were not included in the study of Johnson et al. (2017) but a morphologically very similar sample, *James* 05-35 from Morobe Province, which is also from Section *Geodesme* was included and is resolved as sister to the Pacific clade (Johnson et al., 2017). A lack of sampling in the current study from the intervening areas (Solomon Islands, Fiji and Samoa) may be the explanation for this apparently long-distance dispersal, as Johnson et al. (2017) with more dense sampling of Pacific taxa recovered dispersal events from the Solomon Islands to Fiji, Fiji to the Hawaiian Islands, Fiji/Samoa to the Society Islands, and Samoa to the Marquesas. Clark et al. (2008, 2009) first inferred Fiji and Samoa to be an important biogeographic interface between Southeast Asia and the Pacific, and this was confirmed by the biogeographic analyses of Johnson et al. (2017).

The lack of geographic structure in the phylogeny of New Guinea taxa is notable, with taxa from widely separated areas within New Guinea often resolving as sister, and taxa collected in the same locality falling into well-supported separate clades. For example, *C. bungahijau* which is endemic to Yapen Island in the far north west of Indonesian New Guinea is resolved as sister to *C. subulibracteata* from Morobe Province in Papua New Guinea. Additionally, some species (e.g. *C. vittata*) have very wide distributions, much larger than typically found elsewhere in Malesia (Chapter Two; Atkins et al. 2019). These patterns possibly indicate a shift to bird dispersal, or may signal that these represent very recent radiations on the island and have not yet been subjected to range contractions or extinction.

4.4.3 Borneo as a major evolutionary hotspot

The island of Borneo emerges as the most likely ancestral area for all of the early diverging clades of *Cyrtandra* (Fig. 4.7), and is the source of the highest number of dispersal events in the region, with dispersals to the Philippines, Sulawesi, Sumatra and Peninsular Malaysia (Fig. 4.8). The origin of *Cyrtandra* in Borneo in the middle Miocene, during the global middle Miocene climate and sea-level maximum, followed by lineage accumulation and subsequent high levels of dispersal is consistent with De Bruyn's (De Bruyn et al., 2014) characterisation of the island as a major wet forest refuge and 'evolutionary hotspot' for the region and with Lohman's description of the island as a 'cradle of diversity' (Lohman et al., 2011). The combination of Borneo's large area, relatively stable geological history (Hall, 2012b, De Bruyn et al., 2014), and extensive areas of rainforest even during the glacial maxima (Cannon, 2012), offer the most compelling explanation for this lineage accumulation and *in-situ* diversification.

This pattern of an accumulation of lineages over time in areas of stability, such as Borneo, combined with recent and rapid accumulation of species via high speciation rates (in, for example, the Philippines and New Guinea), triggered by climatic shifts or mountain building, is consistent with findings from the Neotropics where there is evidence that many species-rich tropical groups show episodic species turnover and contain many young species (Antonelli & Sanmartin, 2011, Koenen et al., 2015, Pennington et al., 2015)

Borneo is undoubtedly a centre of diversity for *Cyrtandra*, with approximately 200 species (Atkins et al., 2013) and much undescribed diversity. Burtt (2001a) in his survey of the genus speculated that Borneo represented the 'original heartland' of the genus showing abundant morphological diversity, including richly developed anatomical characters such as sclereids and tracheoids which 'decrease in all directions' from this centre. Biogeographic studies focused on *Cyrtandra* in the Pacific had already shown that the origin of the genus was in Southeast Asia (Clark et al., 2008, 2009, Johnson et al.,

2017) and it is now clear, with greater sampling from the region, that the genus originated on the large island of Borneo.

4.4.4 High levels of floristic exchange on the Sunda shelf

Taxa from localities within the Sunda shelf region (Borneo, Sumatra, Java, Thailand and Peninsular Malaysia) are mixed together in the early diverging clades A, B and C (Fig. 4.4) and the more derived clade F (Fig. 4.5) suggesting regular floristic exchange between these areas. Clade C, for example, contains samples from Borneo, Java, Sumatra, Thailand and Peninsular Malaysia with very little geographic structuring within the clade. The biogeographic stochastic mapping results also suggest regular dispersal between these areas with the highest number of dispersal events from Java to Sumatra (3.1 events) followed by Borneo to Sumatra (2.9), Sumatra to Peninsular Malaysia (2.5), Sumatra to Java (2.1) and Borneo to Peninsular Malaysia (1.9) (Table 4.6; Fig. 4.8).

The high levels of floristic exchange and examples of widespread species shared between the islands that comprise the Sunda shelf reflect the shared geological history of these continental islands. Islands on the shallow continental shelf, would have formed continuous land during at least some of the glacial maxima (Voris, 2000, Hall, 2012). The glacial phases of the Quaternary are estimated to comprise approximately 90% of the past million years (Cannon et al., 2009) so that the situation today is anomalous when considered across this longer timeframe. During the glacial maxima vegetation would also have been very different from the present day with much more extensive areas of rainforest (Cannon, 2012, Cannon et al., 2009, 2014, Morley, 2012) again significantly facilitating exchange and dispersal in these wet forest groups.

The smaller islands of the continental shelf have far fewer species and represent much narrower morphological diversity than that found in Borneo and the Philippines. Sumatra has the richest species diversity after Borneo with ~45 species (Bramley and Cronk, 2003) and many new species still to be described. Basic taxonomic work is still greatly needed, and this is reflected in the large number of samples from Sumatra in the present analysis that have only been named to genus. Areas with lower species diversity include Java with 18 species (Bakhuizen van den Brink 1950), Peninsular Malaysia with nine species (Bramley et al. 2004b) and Thailand with only five species (Burtt 2001b). Burtt (2001a) describes the *Cyrtandra* of Peninsular Malaysia and further north as the ‘tattered fringe of this great genus’ and the result of speciation from a much narrower genetic base. The majority of species on the Sunda shelf are white flowered with or without markings, and with the

exception of *C. stonei*¸ a narrow endemic from Peninsular Malaysia, most have hard, indehiscent fruits presumably dispersed by small mammals

In addition to the four themes discussed above, a number of other patterns emerged. These are discussed in the following sections:

4.4.5 Philippines as a major route through the Malesian region and centre of diversity

We confirm the role of the Philippines as a major route through the region for *Cyrtandra*. In the ancestral range estimation analysis the Philippines is resolved as being the most likely ancestral range for all of the predominantly eastern clades (Clades G, H, I, J, Fig. 4.7) which contain samples from New Guinea, Sulawesi, Taiwan, Japan, the Marquesas and the Hawaiin Islands. Although the rates of floristic exchange on the Sunda Shelf are high, the highest number of dispersal events across the whole analysis is from the Philippines to Sulawesi (3.9 events). Dispersal events from the Philippines are hypothesised north to Taiwan and southern Japan (1.5), a route predicted previously by Kokubugata et al. (2010), east to New Guinea (0.9), a route reported by Nauheimer et al. (2012) in their study of the plant genus *Alocasia,* and even south-west to Java (1 event).

In their summary of biogeographic patterns in the region, Lohman et al. (2011) highlighted the Philippines as a key route through the centre of the region with 'dispersals into, out of and among Philippine islands' being common. These observations were based mostly on animals (Jones & Kennedy 2008, Lohman et al. 2010) and although a key role for the Philippines has not been highlighted in many other plant studies this probably reflects low sampling from the Philippines, a fact highlighted by Hughes et al., (2015) in their Philippine-focused biogeographic study of *Begonia* where they inferred a late Miocene colonisation of the archipelago via long distance dispersal from western Malesia.

For *Cyrtandra*, the earliest diverging branch of Philippine taxa are from Palawan and Camiguin (Clade G) nearly 10 mya suggesting that the Philippines was colonised relatively early in the diversification of the genus and that both short and longer distance dispersal from Borneo played a part in the colonisation of the archipelago. These results provide some support for the theory that Palawan, or some part of it, could have been above sea level significantly earlier than the start of the Pliocene c 5 mya as proposed for the Palawan Ark Hypothesis (Blackburn et al., 2010, Siler et al., 2012). These results would also require Camiguin to be above sea level earlier than the estimated 2 mya

maximum age for this island (Steppan et al., 2003) although incomplete sampling, particularly from nearby islands in the archipelago, could also explain these discrepancies in dates. The very different position of the Philippine islands 10 mya with southern Philippine islands such as Mindanao located much further south and, therefore, closer to Borneo and Sulawesi (Hall, 2002, Hughes et al., 2015), offers some explanation for the role of the Philippines as a major route through the region from Borneo to New Guinea.

The Philippines is another centre of diversity for the genus with 150 species and new species still being described (Olivar et al., accepted.). Species from these islands are morphologically very diverse from small, mat-forming herbs such as *C. auriculata* to epiphytes such as *C. angularis* and large, densely villose shrubs such as *C. villosissima*. They comprise both very narrow endemics such as *C. cleopatrae*, which is restricted to a single mountain in Palawan and more widespread species such as *C. cumingii,* which is reported from several islands. Flower colour is much more diverse than on the Sunda shelf with yellow, red and pink flowers recorded. There are a number of examples of fleshy fruits in the Philippines, notably *C. hirtigera* from Palawan and *C. fragilis* from Negros and Mindanao, which is congruent with the high vagility of lineages in Philippine clades.

4.4.6 Sulawesi shows exceptional levels of immigration and emerges as a 'sink' island

Sulawesi is an area of significant immigration being the recipient of 20% of all dispersals, the second highest recorded in our analysis (Table 4.6). This includes dispersals from Java, the Philippines and Borneo. In contrast dispersal events from Sulawesi to surrounding islands are very low (0.47 events to Sumatra and 0.17 events to the Philippines being the highest) Table 4.6, Fig 4.8). The phenomenon of geologically younger or recently emergent islands, such as Java, showing increased levels of immigration is documented by De Bruyn et al. (2014) in their meta-analysis of the Southeast Asian flora. Determining the age of Sulawesi is problematic (Hall, 2009). Although Sulawesi only arrived at its current position, and composition, in the last 5 my (Hall, 2009, Stelbrink et al., 2010) fragments of the island have been present far longer; West Sulawesi dating back to the Eocene and possibly earlier although when it was submerged is not completely clear (Hall, 2009, Stelbrink et al., 2010). Conversely, some of the islands of the Philippine archipelago that appear to play a key role as a source of dispersals in the genus are very young; for example, Camiguin is reported to be only 2 mya (Steppan et al., 2003). The earliest arrivals of *Cyrtandra* to Sulawesi are also not particularly recent, potentially arriving as early as7 mya (Fig. 4.6). Sulawesi is relatively low in species number (c. 40 species) compared to the very high diversity of the nearby islands of Borneo (200 species) and the Philippines (150 species) thereby providing a much smaller pool of potential dispersers. Improved

observations on number of individuals as well as number of species would be useful as this is also likely to be an important factor. The floral morphological diversity is much more varied than on the Sunda shelf with deep red, yellow, purple and striped flowers present (Fig. 4.2 a-f) and some unusual corolla shapes including species such as *C. purpurea* with a greatly elongated and recurved lower lobe more typical of Section *Glossophorae* in New Guinea. It is notable that although fleshy fruited *Cyrtandra* species, such as the unusual epiphytic *C. purpurea,* occur in Sulawesi, many of the most common species on the island, such as *C. hypogaea, C. polyneura* and *C. kinhoii* are characterised by the drier, tough-walled fruits typical of the Sunda shelf. There is even one species, *C. tenuicarpa* with the very narrow, linear fruits that are typically found in Borneo. This low level of emigration and the relative insignificance of Sulawesi in terms of a dispersal route across the region is, however, also seen in *Begonia* (Thomas et al., 2012) and observed by Stelbrink et al. (2012) in their paper on the origin of the Sulawesi fauna. Sulawesi is encircled by biogeographic boundaries, including Wallace's and Huxley's line to the west, and Weber's and Lydekker's to the east suggesting that there are real barriers to dispersal in this area although immigration on to the island, particularly from the Philippines and Borneo across at least the western lines, has clearly occurred more than once in *Cyrtandra*. Dispersal back across Wallace's line from Sulawesi and successful establishment on the Sunda shelf islands appears to have been difficult for *Cyrtandra,* perhaps due to niche pre-emption in the older and more established floras of these islands, although there is one example of dispersal from the Philippines to Java recorded in this analysis. The presence of a more seasonal climate, or poor sampling, from the islands immediately to the east of Sulawesi, notably the Moluccas, may explain why so few examples of successful colonisation events are detected in this direction although, with many examples of long distance dispersal recorded in the evolution of the genus it is perhaps surprising that there are no instances of Sulawesi to New Guinea emigrations. Increased sampling of *Cyrtandra* from the Moluccas and New Guinea may help illuminate whether this is a real barrier or whether it is an artefact of low sampling.

4.4.7 Java as an anomalous island with links to both the Sunda shelf and Wallacea

In this study, seven of the nine species from Java included in the analysis resolve in the predominantly Sunda clades (Clades C and F, Fig. 4.4 & 4.5). However, there are two Javan species, *C. sulcata* and *C. coccinea,* collected in Central Java, which fall into the eastern Malesian clade, sister to two species from Sulawesi (see Clade J, Fig. 4.5). These are the only two Sunda species in the predominantly Wallacean clade (Clade J, Fig. 4.5). Using phenetic analyses of plant species distributions, van Welzen et al. (2011), partitioned Malesia in to three phytogeographic regions with Java as a somewhat anomalous Sunda shelf island with its flora showing stronger affinities with the

floras of the islands of Wallacea such as Sulawesi and the Philippines than might be expected given the shared geological history of the Sunda shelf. Van Welzen et al. (2011) speculated that this may be due to the more seasonal climate, particularly of central and eastern Java. The two Javan species in the Wallacean clade, *C. coccinea* and *C. sulcata* both have broad ecological niches, are widespread on Java, and have wide altitudinal ranges from 200 to 2000 m making them potentially good dispersers and colonisers. Whereas most of the species on Java have morphological affinities with those of the Sunda shelf, and some such as *C. sandei* have distributions that span both Java and Sumatra, *C. coccinea* appears to be part of a group of *Cyrtandra* species that share distinctive ovate leaves and reddish colouring in the leaves and reproductive structures (including *C. celebica* from Sulawesi, *C. vulcanica* from the Philippines and *C. phoenicea* from Seram) that have their centre of diversity further to the east.

Improved understanding of range sizes in *Cyrtandra* and their distribution, both geographically and phylogenetically, will be helpful in the interpretation of these biogeographic patterns and, specifically, whether the prevalence of widespread species on islands such as Java, and the apparent lack of them on Sulawesi, for example, may be an important part of the explanation for these island's different dispersal histories. Increased collections and availability of accurately georeferenced specimen information should allow more accurate analysis of this in the future.

4.9 Conclusion

Using a robust phylogenetic framework to study evolutionary relationships and biogeographical processes in Southeast Asian *Cyrtandra*, we found evidence in support of all four of the emerging themes in Southeast Asian biogeography: 1) Increased diversification across the region from the late Miocene, 2) West to east dispersal, 3) Borneo as a major evolutionary hotspot, and 4) High levels of floristic exchange on the Sunda shelf. In addition, our findings suggest a key role for the Philippines as a major route through the region, Sulawesi as an island of high immigration, and Java as an island with links both to the Sunda shelf and Wallacea. The present study has provided further insight into the fundamental questions of when and where plant diversification took place in Southeast Asia, and the role of geo-tectonic and climatic processes in shaping the region and setting the stage for significant species diversifications. Further work is needed at the level of the niche and the genome to unravel how the massive species richness of *Cyrtandra* evolved and how it is maintained.

Acknowledgements

We acknowledge financial support for this research from the Edinburgh Botanic Garden (Sibbald) Trust, and the Elvin McDonald Research Endowment Fund (The Gesneriad Society). The Royal Botanic Garden Edinburgh is supported by the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government. Funding for fieldwork was provided by the RBGE Travel Fund, the James & Eve Bennett Trust, the Royal Horticultural Society and Davis Expedition Fund.

A large number of collaborators and organisations have assisted the authors in the field over many years. In Indonesia, we would like to thank RISTEKDIKTI, the Indonesian Ministry of Forestry and staff at the Kebun Raya Bogor, Herbarium Bogoriense, Forestry Research Institute of Manado and Andalas University particularly Joeni Rahajoe, Wisnu Ardi, Marlina Ardiyani, Hendrian, Julianus Kinho, Deden Girmansyah and Nurainas. In Malaysia, we would like to thank staff at the Forest Research Institute Malaysia, particularly Ruth Kiew and Sam Yen Yen, the Tree Flora of Sabah and Sarawak programme, Postar Miun, Joan Pereira, Susana Sabran and Julia Sang). Fieldwork in the Philippines over many years was facilitated by the Philippine National Herbarium.

In addition to collections made by the authors additional samples were generously provided by RBG Kew, Shelley James (Florida Museum of Natural History, Bishop Museum, Honolulu), Wisnu Ardi (Bogor Botanic Garden), Deden Girmansyah (Herbarium Bogoriense), M. Poopath (Thailand) and Michael Kiehn (Vienna Botanic Garden). Over many years of fieldwork, current and former RBGE staff and students, have also collected a large number of *Cyrtandra* collections as part of RBGE expeditions for which we are very grateful. These include (in alphabetical order) George Argent, Sadie Barber, B.L.Burtt, Quentin Cronk, Andy Ensoll, Louise Galloway, Olive Hilliard, Mary Mendum, David Middleton, Mark Newman, Axel Poulsen, Carmen Puglisi, Steve Scott, Daniel Thomas and Peter Wilkie.

We would like to thank Prof Gao Lianming, Kunming Institute of Botany, Chinese Academy of Sciences, Yunnan, China, for the gift of cpDNA sequences of two of the outgroup samples.

At RBGE, we would like to thank Steve Scott, Sadie Barber and Nathan Kelso for excellent care of the *Cyrtandra* living collections over many years. We thank Michelle Hart, Laura Forrest and Ruth Hollands for expert advice in the molecular laboratories at RBGE. Assistance with the programme BioGeoBEARS was generously given by Nick Matzke. Thanks also to Jay Edneil Olivar for enormous help with naming of the Philippine samples included in the analysis.

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Appendix 4.1**. Taxon list for samples in the current study including six outgroup species.** Ingroup samples are listed in alphabetical order by taxon name following the six outgroup taxa. Voucher details, locality and herbarium are given for each sample. GenBank accession numbers are included for each of the five genic regions. The * symbol indicates where no sequence data was obtained. Those sequencs generated by HA are in bold and italicised.

Species	Collector and Number	Herb	Locality	ITS	TrnLF	psbA-trnH	rpl32	matK
Aeschynanthus buxifolius	Goodwin & Cherry 384	E	Vietnam	MN843191	MN842996	MN843568	MN842817	MN843507
Aeschynanthus roseoflorus	Argent 87/14	E	Seram	MN843190	MN842995	MN843567	MN842816	MN843508
Agalmyla chalmersii	Chapman sn (RBGE acc no. 19661971)	E	New Guinea	MN843192	MN842997	MN843569	MN842818	MN843380
Billolivia violacea	South Vietnam First Darwin Expedition 201	E	Vietnam	MN843193	MN842994	MN843570	MN842819	*
Didymocarpus antirrinoides	Jong 9009 (RBGE acc no. 19650167)	E	Malaysia	MN843189	MN842994	MN843566	MN842815	MN843382
Loxostigma griffithii	Kew Edinburgh Kanchenjunga Expedition	E	Nepal	MN843194	MN842999	MN843571	MN842820	MN843509
C. aff *bracteata*	Utteridge 91	K	New Guinea	***MN843243***	***MN843049***	MN843616	MN842864	MN843427
C. aff *disparoides*	Wilkie et al SFC-07445	E	Borneo	***MN843211***	***MN843015***	MN843588	MN842837	MN843543
C. aff *erectiloba*	James 586	BISH	New Guinea	***MF446067***	***MN843060***	MF446277	MF509475	MN843546
C. aff *multinervis*	Argent et al 159	E	Sulawesi	***MN843292***	***MN843101***	MN843663	MN842910	MN843455
C. aff *picta*	Hughes et al SUBOE 78	E	Sumatra	***MN843349***	***MN843158***	MN843718	MN842965	MN843519
C. aff *ramiflora*	Mendum et al 29009	E	Philippines	***MN843269***	***MN843078***	*	*	MN843469
C. aff *rosea*	Hughes et al SUBOE 20	E	Sumatra	***MN843341***	***MN843150***	MN843710	MN842957	MN843513
C. aff *rosea*	Radhiah & Cronk 53	E	Sumatra	***MN843365***	***MN843174***	MN843734	*	MN843480
C. aff *rosea*	Radhiah & Cronk 55	E	Sumatra	***MN843366***	***MN843175***	MN843735	MN842981	MN843482
C. aff *ferruginea*	Mendum et al 29053	E	Philippines	***MN843273***	***MN843082***	MN843644	MN842893	MN843470
C. albiflora	Scott 509 (RBGE acc no 20040645)	E	Sulawesi	***MN843293***	***MN843102***	MN843664	*	MN843501
C. anisophylla	Radhiah & Cronk 109	E	Sumatra	***MN843335***	***MN843144***	MN843704	MN842952	MN843486
C. arachnoidea	Cronk, Burtt, Hilliard & Mendum CBHM 27	E	Borneo	***MN843197***	*	MN843573	MN842822	MN843451
C. areolata	Mendum, M. MM 52	E	Borneo	***MN843198***	***MN843001***	MN843574	MN842823	MN843420
C. aurantiaca	Cronk, Burtt, Hilliard & Mendum CBHM 23	E	Borneo	***MN843199***	***MN843002***	MN843575	MN842824	MN843496
C. aureotincta	Radhiah & Cronk 122	E	Sumatra	***MN843336***	***MN843145***	MN843705	MN842953	MN843491
C. baileyi	Cronk & Percy T118	E	Australia	***MN843195***	*	*	*	*
C. boliohutensis	Scott 505 (RBGE acc no 20021906)	E	Sulawesi	***MN843294***	***MN843103***	MN843665	MN842911	MN843384
C. boliohutensis	Argent et al 196	E	Sulawesi	***MN843295***	***MN843104***	MN843666	MN842912	MN843457
C. boliohutensis	Atkins et al 188	E	Sulawesi	***MN843296***	***MN843105***	MN843667	MN842913	MN843467

C. bungahijau	Atkins 57 (RBGE acc no 20090826)	E	New Guinea	***MN843249***	***MN843055***	MN843622	MN842870	MN843433
C. burbidgei	Cronk, Burtt, Hilliard & Mendum CBHM 21	E	Borneo	***MN843200***	***MN843003***	MN843576	MN842825	MN843449
C. burbidgei	Cronk, Burtt, Hilliard & Mendum CBHM 22	E	Borneo	***MN843201***	***MN843004***	MN843577	MN842826	MN843450
C. calyptribracteata	Moller sn (RBGE acc no 19973430)	E	Java	***MN843232***	***MN843036***	MN843605	MN842855	*
C. celebica	Thomas & Ardi 08-50	E	Sulawesi	***MN843297***	***MN843106***	MN843668	MN842914	MN843404
C. celebica	Argent et al 129	E	Sulawesi	***MN843298***	***MN843107***	MN843669	MN842915	MN843453
C. celebica	Barber et al BAKK 12	E	Sulawesi	***MN843300***	***MN843109***	MN843671	MN842917	MN843533
C. celebica	Barber et al BAKK 8	E	Sulawesi	***MN843299***	***MN843108***	MN843670	MN842916	MN843532
C. cf *bracheia*	Wilkie et al SFC-07447	E	Borneo	***MN843212***	***MN843016***	*	*	MN843558
C. cf *carnosa*	Girmansayah 17	E	Sumatra	***MN843355***	***MN843164***	MN843724	MN842971	MN843472
C. cf *cuprea*	Wilkie et al SFC-07404	E	Borneo	***MN843210***	***MN843014***	MN843587	MN842836	MN843542
C. cf *multifolia*	RBGE Philippines IS44	E	Philippines	***MN843268***	***MN843077***	MN843640	MN842889	MN843387
C. cf *patula*	Hughes et al SUBOE 12	E	Sumatra	***MN843337***	***MN843146***	MN843706	MN842954	*
C. cf *patula*	Hughes et al SUBOE 29	E	Sumatra	***MN843338***	***MN843147***	MN843707	MN842955	MN843515
C. cf *pauciflora*	Hoover ARS173	US	Java	***MN843234***	***MN843039***	MN843607	*	MN843544
C. cf *reinwardtii*	Wiriadanata 12709	US	Java	***MN843230***	***MN843034***	MN843603	MN842853	*
C. cf *roseo-alba*	Cronk MAK1	E	Philippines	***MN843267***	***MN843076***	MN843639	MN842888	MN843399
C. chalcodea	James 1232	BISH	New Guinea	***MN843252***	***MN843058***	MN843624	MN842873	MN843505
C. chrysea	Mendum MM58	E	Borneo	***MN843206***	***MN843009***	MN843583	MN842832	MN843421
C. clarkei	Cronk, Burtt, Hilliard & Mendum CBHM 19	E	Borneo	***MF446060***	***MN843010***	MF446268	MF509462	MN843381
C. cleopatrae	Cronk et al 25437	E	Philippines	***MN843274***	***MN843083***	MN843645	*	MN843468
C. coccinea	Hoover ARS167	US	Java	***EU919972***	***MN843037***	GQ475131	MF509463	MN843550
C. connata	Cronk & Percy T92	E	Society Is	***MN843259***	***MN843068***	MN843631	MN842880	MN843393
C. connata	Cronk & Percy T93	E	Society Is	***MN843260***	***MN843069***	MN843632	MN842881	*
C. corniculata	Cronk, Burtt, Hilliard, Mendum CBHM 9	E	Borneo	***MN843207***	***MN843011***	MN843584	MN842833	MN843400
C. crockerella	Mendum MM 43	E	Borneo	***MN843208***	***MN843012***	MN843585	MN842834	MN843417
C. cumingii	RBGE Philippines 99206	E	Philippines	***MN843278***	***MN843087***	MN843649	*	MN843395
C. cupulata	Atkins 59 (RBGE acc no 20010490)	E	Peninsular Malaysia	***MN843282***	***MN843091***	MN843653	MN842900	MN843436
C. cupulata	Phoon FRI53377	BKF	Peninsular Malaysia	***MN843283***	***MN843092***	MN843654	MN842901	MN843471
C. cupuluta	Bramley et al GB28	E	Peninsular Malaysia	***MN843284***	***MN843093***	MN843655	MN842902	MN843424
C. dispar	Wilkie PW 642	E	Sumatra	***MN843342***	***MN843151***	MN843711	MN842958	MN843392
C. dispar	Puglisi et al CP 247	E	Sumatra	***MN843344***	***MN843153***	MN843713	MN842960	MN843443

C. dispar	Radhiah & Cronk 58	E	Sumatra	***MN843345***	***MN843154***	MN843714	MN842961	MN843483
C. dispar	Hughes et al SUBOE 13	E	Sumatra	***MN843347***	***MN843156***	MN843716	MN842963	MN843512
C. disparoides	Church 292	E	Borneo	***MN843209***	***MN843013***	MN843586	MN842835	MN843498
C. elatostemmoides	Puglisi CP302	E	Philippines	***MN843275***	***MN843084***	MN843646	MN842894	MN843414
C. engleri	Scott & Cubey 228 (RBGE acc no 20021223)	E	Sulawesi	***MN843290***	***MN843099***	MN843661	MN842908	MN843434
C. engleri	Atkins et al 202	E	Sulawesi	***MN843291***	***MN843100***	MN843662	MN842909	MN843499
C. erectiloba	James 134	BISH	New Guinea	***MF446066***	***MN843059***	MF446275	MF509473	MN843545
C. eriophylla	Sands 7158	K	New Guinea	***MN843241***	***MN843047***	MN843614	MN842862	MN843425
C. eriophylla	Johns 10040	K	New Guinea	***MN843242***	***MN843048***	MN843615	MN842863	MN843426
C. eriophylla	Utteridge 162	K	New Guinea	***MN843244***	***MN843050***	MN843617	MN842865	MN843428
C. eriophylla	Argent 533	E	New Guinea	***MN843250***	***MN843056***	MN843623	MN842871	MN843503
C. fasciata	Argent et al 198	E	Sulawesi	***MN843303***	***MN843112***	MN843674	MN842920	MN843459
C. fasciata	Atkins et al 54	E	Sulawesi	***MN843304***	***MN843113***	MN843675	MN842921	MN843464
C. feaniana	Percy CM1	E	Marquesas	***MN843255***	***MN843064***	MN843627	MN842876	MN843411
C. fenestrata	Radhiah & Cronk 147	E	Sumatra	***MN843351***	***MN843160***	MN843720	MN842967	MN843555
C. ferruginea	Cubey & Scott 226 (RBGE acc no 19972533)	E	Philippines	***MN843270***	***MN843079***	MN843641	MN842890	MN843437
C. filibracteata	James 1770	BISH	Solomon Islands	***MN843258***	***MN843067***	MN843630	MN842879	MN843564
C. floccosa	Thomas & Ardi 09-90	E	Sulawesi	***MN843305***	***MN843114***	MN843676	MN842922	MN843406
C. fulvisericea	Cronk, Burtt, Hilliard & Mendum CBHM 13	E	Borneo	***MN843213***	***MN843017***	MN843589	MN842838	MN843447
C. fulvisericea	Cronk, Burtt, Hilliard & Mendum CBHM 16	E	Borneo	***MN843214***	***MN843018***	MN843590	MN842839	MN843448
C. geocarpa	Atkins 12 (RBGE acc no 20021222)	E	Sulawesi	***MN843306***	***MN843115***	MN843677	MN842923	MN843388
C. geocarpa	Barber et al BAKK 25	E	Sulawesi	***MN843307***	***MN843116***	MN843678	MN842924	*
C. gibbsiae	Cronk, Burtt, Hilliard, Mendum CBHM 11	E	Borneo	***MN843215***	***MN843019***	MN843591	MN842840	MN843401
C. gibbsiae	Mendum, M. MM 61	E	Borneo	***MN843216***	***MN843020***	MN843592	MN842841	MN843548
C. gorontaloensis	Barber et al BAKK 68	E	Sulawesi	***MN843302***	***MN843111***	MN843673	MN842919	MN843540
C. gorontaloensis	Atkins et al 91	E	Sulawesi	***MN843308***	***MN843117***	MN843679	MN842925	MN843466
C. hedraiantha	de Kok 1239	K	New Guinea	***MN843246***	***MN843052***	MN843619	MN842867	MN843430
C. hendrianii	Scott 503 (RBGE acc no 20040646)	E	Sulawesi	***MN843309***	***MN843118***	MN843680	MN842926	MN843500

C. hirtigera	Cronk et al 25518	E	Philippines	***MN843276***	***MN843085***	MN843647	MN842895	MN843556
C. hirtigera	Cronk et al 25433	E	Philippines	***MN843277***	***MN843086***	MN843648	MN842896	MN843549
C. hispidula	Thomas & Ardi 09-86	E	Sulawesi	***MN843310***	***MN843119***	MN843681	MN842927	*
C. hypogaea	Scott 449 (RBGE acc no 20040647)	E	Sulawesi	***MN843311***	***MN843120***	MN843682	MN842928	MN843383
C. hypogaea	Barber et al BAKK 17	E	Sulawesi	***MN843312***	***MN843121***	*	MN842929	MN843534
C. impressivenia	Radhiah & Cronk 116	E	Sumatra	***MN843352***	***MN843161***	MN843721	MN842968	MN843490
C. incisa	Cronk MAK4	E	Philippines	***MN843271***	***MN843080***	MN843642	MN842891	MN843445
C. incompta	Radhiah & Cronk 50	E	Sumatra	***MN843353***	***MN843162***	MN843722	MN842969	MN843479
C. keithii	Bramley et al SAN147235	K	Borneo	***MN843218***	*	MN843581	MN842830	MN843526
C. kermesina	Cronk, Burtt, Hilliard & Mendum CBHM 8	E	Borneo	***MN843217***	***MN843021***	MN843593	MN842842	MN843446
C. kermesina	Cronk, Burtt, Hilliard & Mendum CBHM 14	E	Borneo	***MN843219***	***MN843022***	MN843594	MN842843	MN843494
C. kinhoi	Atkins et al 56	E	Sulawesi	***MN843313***	***MN843122***	MN843683	MN842930	MN843465
C. kinhoi	Barber et al BAKK 36	E	Sulawesi	***MN843314***	***MN843123***	MN843684	MN842931	MN843536
C. kinhoi	Barber et al BAKK 65	E	Sulawesi	***MN843315***	***MN843124***	*	MN842932	MN843539
C. lagunae	Cronk MAK3	E	Philippines	***MN843272***	***MN843081***	MN843643	MN842892	MN843444
C. lanata	Cronk, Burtt, Hilliard & Mendum CBHM 20	E	Borneo	***MN843220***	***MN843023***	*	*	MN843495
C. longistamina	Argent et al 197	E	Sulawesi	***MN843301***	***MN843110***	MN843672	MN842918	MN843458
C. luteiflora	Atkins et al 52	E	Sulawesi	***MN843316***	***MN843125***	MN843685	MN842933	MN843463
C. mendumiae	Mendum MM 46	E	Borneo	***MN843221***	***MN843024***	MN843595	MN842844	MN843419
C. mesilauensis	Cronk, Burtt, Hilliard, Mendum CBHM 7	E	Borneo	***MN843222***	***MN843025***	*	MN842845	MN843402
C. mesilauensis	Cronk, Burtt, Hilliard & Mendum CBHM 6	E	Borneo	***MF446095***	***MN843026***	MN843596	MN842846	MN843493
C. mollis	Barber et al BAKK 42	E	Sulawesi	***MN843317***	***MN843126***	MN843686	MN842934	MN843557
C. mollis	Barber et al BAKK 83	E	Sulawesi	***MN843318***	***MN843127***	MN843687	MN842935	MN843541
C. mooreaensis	Cronk & Percy T26	E	Society Is	***MN843261***	***MN843070***	MN843633	MN842882	*
C. nitida	Argent et al 111	E	Sulawesi	***MN843319***	***MN843128***	MN843688	MN842936	MN843452
C. nukuhivensis	Percy CM4	E	Marquesas	***MN843256***	***MN843065***	MN843628	MN842877	MN843413
C. oblongifolia	Scott 506 (RBGE acc no 19912412)	E	Borneo	***MN843223***	***MN843027***	MN843597	MN842847	MN843415
C. oligantha	Radhiah & Cronk 68	E	Sumatra	***MN843356***	***MN843165***	MN843725	MN842972	MN843422
C. oligantha	Radhiah & Cronk 54	E	Sumatra	***MN843357***	***MN843166***	MN843726	MN842973	MN843481
C. oligantha	Hughes et al SUBOE 10	E	Sumatra	***MN843358***	***MN843167***	MN843727	MN842974	MN843511
C. ootensis	Percy CM3	E	Marquesas	***MN843257***	***MN843066***	MN843629	MN842878	MN843412
C. pallida	RBGE Philippines 99219	E	Philippines	***MN843279***	***MN843088***	MN843650	MN842897	MN843396

C. patula	Bramley et al GB36	E	Peninsular Malaysia	***MN843285***	***MN843094***	MN843656	MN842903	MN843478
C. pauciflora	Hughes et al SUBOE 70	E	Sumatra	***MN843339***	***MN843148***	MN843708	*	MN843517
C. pauciflora	Hughes et al SUBOE 72	E	Sumatra	***MN843340***	***MN843149***	MN843709	MN842956	MN843518
C. peltata	Radhiah & Cronk 71	E	Sumatra	***MN843359***	***MN843168***	MN843728	MN842975	MN843484
C. pendula	Atkins 4	E	Java	***MN843235***	***MN843040***	MN843608	MN842857	MN843439
C. pendula	Bramley et al GB37	E	Peninsular Malaysia	***MN843286***	***MN843095***	MN843657	MN842904	MN843565
C. pendula	Radhiah & Cronk 74	E	Sumatra	***MN843360***	***MN843169***	MN843729	MN842976	MN843552
C. pendula	Hughes et al SUBOE 28	E	Sumatra	***MN843361***	***MN843170***	MN843730	MN842977	MN843514
C. pendula	Middleton et al 5447	E	Thailand	***MN843373***	***MN843182***	MN843742	MN842988	MN843441
C. pendula	Middleton et al 3950	E	Thailand	***MN843374***	***MN843183***	MN843743	MN842989	MN843442
C. pendula	Poopath MP60	BKF	Thailand	***MN843375***	***MN843184***	MN843744	MN842990	MN843474
C. pendula	Wilkie PW925	E	Thailand	***MN843376***	***MN843185***	MN843745	*	MN843506
C. picta	Radhiah & Cronk 66	E	Java	***MN843236***	***MN843041***	MN843609	MN842858	MN843553
C. picta	Atkins 2	E	Java	***MN843237***	***MN843042***	MN843610	MN842859	MN843438
C. picta	Radhiah & Cronk 108	E	Sumatra	***MN843354***	***MN843163***	MN843723	MN842970	MN843485
C. polyneura	Thomas & Ardi 08-25	E	Sulawesi	***MN843320***	***MN843129***	MN843689	MN842937	MN843403
C. polyneura	Argent et al 217	E	Sulawesi	***MN843321***	***MN843130***	MN843690	MN842938	MN843561
C. polyneura	Atkins et al 40	E	Sulawesi	***MN843322***	***MN843131***	MN843691	MN842939	MN843462
C. polyneura	Barber et al BAKK 41	E	Sulawesi	***MN843323***	***MN843132***	MN843692	MN842940	MN843537
C. purpureofucata	Thomas & Ardi 09-88	E	Sulawesi	***MN843324***	***MN843133***	MN843693	MN842941	MN843405
C. purpureofucata	Argent et al 252	E	Sulawesi	***MN843325***	***MN843134***	MN843694	MN842942	MN843461
C. rantemarioensis	Thomas & Ardi 09-81	E	Sulawesi	***MN843326***	***MN843135***	MN843695	MN842943	MN843407
C. rantemarioensis	Thomas & Ardi 09-79	E	Sulawesi	***MN843327***	***MN843136***	MN843696	MN842944	MN843408
C. rantemarioensis	Argent et al 240	E	Sulawesi	***MN843328***	***MN843137***	MN843697	MN842945	MN843460
C. rhyncanthera	Radhiah & Cronk 111	E	Sumatra	***MN843362***	***MN843171***	MN843731	MN842978	MN843488
C. rosea	Radhiah & Cronk 115	E	Sumatra	***MN843363***	***MN843172***	MN843732	MN842979	*
C. roseiflora	Argent et al 173	E	Sulawesi	***MN843329***	***MN843138***	MN843698	MN842946	MN843456
C. rostrata	Radhiah & Cronk 162	E	Java	***MN843238***	***MN843043***	MN843611	*	MN843410
C. rubriflora	Wilkie PW 603	E	Sumatra	***MN843364***	***MN843173***	MN843733	MN842980	MN843391
C. sandei	Atkins 5	E	Java	***MN843239***	***MN843044***	MN843612	MN842860	MN843440
C. sandei	Hughes et al SUBOE 93	E	Sumatra	***MN843367***	***MN843176***	MN843736	MN842982	MN843520
C. sect. *Geodesme*	de Kok 1266	K	New Guinea	***MN843248***	***MN843054***	MN843621	MN842869	MN843432
C. sect. *Geodesme*	Argent 609	E	New Guinea	***MN843251***	***MN843057***	*	MN842872	MN843504
C. serratifolia	Atkins et al 93	E	Sulawesi	***MN843330***	***MN843139***	MN843699	MN842947	*
C. serratifolia	Barber et al BAKK 44	E	Sulawesi	***MN843331***	***MN843140***	MN843700	MN842948	MN843538
C. sibuyanensis	RBGE Philippines 99218	E	Philippines	***MN843280***	***MN843089***	MN843651	MN842898	MN843397
C. sinclairiana	Cronk, Burtt, Hilliard, Mendum CBHM 1	E	Borneo	***MN843224***	***MN843028***	MN843598	MN842848	*
C. smithiana	Mendum MM30	E	Borneo	***MN843225***	***MN843029***	MN843599	MN842849	MN843418

C. smithiana	Bramley et al SAN147245	E	Borneo	***MN843205***	***MN843008***	MN843582	MN842831	MN843525
C. smithiana	Cronk, Burtt, Hilliard & Mendum CBHM 25	E	Borneo	***MN843226***	***MN843030***	MN843600	MN842850	MN843497
C. sojolensis	Argent et al 158	E	Sulawesi	***MN843332***	***MN843141***	MN843701	MN842949	MN843454
C. sp 1	Bramley et al SAN147207	K	Borneo	***MN843203***	***MN843006***	MN843579	MN842828	MN843524
C. sp 2	RBGE Philippines 99211	E	Philippines	***MN843281***	***MN843090***	MN843652	MN842899	MN843398
C. sp 3	Bramley et al SAN147205	K	Borneo	***MN843202***	***MN843005***	MN843578	MN842827	MN843523
C. sp 4	Bramley et al SAN147222	K	Borneo	***MN843204***	***MN843007***	MN843580	MN842829	MN843527
C. sp 5	Hughes et al SUBOE 9	E	Sumatra	***MN843346***	***MN843155***	MN843715	MN842962	MN843510
C. sp 6	Hughes et al SUBOE 41	E	Sumatra	***MN843348***	***MN843157***	MN843717	MN842964	MN843516
C. sp 7	Wiriadanata 12713	US	Java	***MN843231***	***MN843035***	MN843604	MN842854	MN843522
C. sp 8	Wilkie PW 760	E	Sumatra	***MN843343***	***MN843152***	MN843712	MN842959	MN843390
C. sp 9	Argent & Smith 11	E	Bali	***MN843196***	***MN843000***	MN843572	MN842821	MN843502
C. sp 10	Radhiah & Cronk 168	E	Java	***MN843233***	***MN843038***	MN843606	MN842856	MN843409
C. sp 11	Hughes et al SUBOE 96	E	Sumatra	***MN843350***	***MN843159***	MN843719	MN842966	MN843521
C. sp 12	Kiehn 940808	W	Hawaii	***MN843254***	***MN843063***	MN843626	MN842875	MN843394
C. splendens	Clark 820		Borneo	***MN843227***	***MN843031***	*	*	MN843559
C. stenoptera	Radhiah & Cronk 145	E	Sumatra	***MN843368***	***MN843177***	MN843737	MN842983	MN843423
C. stenoptera	Radhiah & Cronk 110	E	Sumatra	***MN843369***	***MN843178***	MN843738	MN842984	MN843487
C. stenoptera	Radhiah & Cronk 113	E	Sumatra	***MN843370***	***MN843179***	MN843739	MN842985	MN843489
C. stonei	Bramley et al GB34	E	Peninsular Malaysia	***MN843287***	***MN843096***	MN843658	MN842905	MN843477
C. subulibractea	James 408	BISH	New Guinea	***MN843253***	***MN843061***	MN843625	MN842874	MN843563
C. subulibractea	James 445	BISH	New Guinea	***MF446138***	***MN843062***	MF446344	MF509567	MN843547
C. sulcata	Hoover ARS160	US	Java	***EU919980***	***MN843045***	GQ475132	MF509569	MN843551
C. tenuicarpa	Argent et al 229	E	Sulawesi	***MN843333***	***MN843142***	MN843702	MN842950	MN843560
C. teysmannii	Radhiah & Cronk 87	E	Sumatra	***MN843371***	***MN843180***	MN843740	MN842986	MN843562
C. trichodon	Radhiah & Cronk 124	E	Sumatra	***MN843372***	***MN843181***	MN843741	MN842987	MN843492
C. umbellifera	Kokubugata GK15859	TNS	Philippines	***MN843265***	***MN843074***	MN843637	MN842886	MN843530
C. umbellifera	Kokubugata GK6031	TNS	Taiwan	***MN843379***	***MN843188***	MN843748	MN842993	MN843528
C. villosissima	CULTE 16108 (RBGE acc no 19991945)	E	Philippines	***MN843264***	***MN843073***	MN843636	MN842885	MN843416
C. villosissima	RBGE Philippines 99316	E	Philippines	***MN843266***	***MN843075***	MN843638	MN842887	MN843554
C. vittata	Atkins 14 (RBGE acc no 20090734)	E	New Guinea	***MN843240***	***MN843046***	MN843613	MN842861	MN843385
C. vittata	de Kok 1156	K	New Guinea	***MN843245***	***MN843051***	MN843618	MN842866	MN843429

C. vittata	de Kok 1263	K	New Guinea	***MN843247***	***MN843053***	MN843620	MN842868	MN843431
C. wallichii	Bramley et al GB25	E	Peninsular Malaysia	***MN843288***	***MN843097***	MN843659	MN842906	MN843475
C. wallichii	Bramley et al GB33	E	Peninsular Malaysia	***MN843289***	***MN843098***	MN843660	MN842907	MN843476
C. wallichii	Atkins 41 (RBGE acc no 20090366)	E	Thailand	***MN843377***	***MN843186***	MN843746	MN842991	MN843389
C. wallichii	Poopath MP187	BKF	Thailand	***MN843378***	***MN843187***	MN843747	MN842992	MN843473
C. widjajae	Barber et al BAKK 32	E	Sulawesi	***MN843334***	***MN843143***	MN843703	MN842951	MN843535
C. yaeyamae	Kokubugata GK18916	TNS	Japan	***MN843229***	***MN843033***	MN843602	MN842852	MN843531
C. yaeyamae	Scott 501 (RBGE acc no 20031648A)	E	Japan	***MN843263***	***MN843072***	MN843635	MN842884	MN843386

Chapter Five: Conclusions and Future work

The research presented in this thesis has given insights in to the taxonomy and diversification of one of the most species-rich and emblematic genera of the Southeast Asian rain forest. Accurately documenting species diversity and discovering when and where speciation took place are important steps towards unravelling the key questions of how so many species arose in *Cyrtandra* and how they are maintained. The principal achievements of this dissertation are:

1. From a new taxonomic revision of the *Cyrtandra* on Sulawesi (Chapter Two) we have much more detailed information about the diversity of *Cyrtandra* on one of the major islands at the centre of diversity of the genus. The revision covers 40 species, five of which are new; plus a key to the species, illustrations and photographs of 36 species, distribution maps for all species and preliminary conservation assessments. Of the 40 Sulawesi species, 38 are endemic, two are also recorded from Java and Sumatra. Provisional conservation assessments suggest that two of these species are Critically Endanagered, one is Endangered, thirteen are Vulnerable, one is Near Threatened and 22 are of Least concern. Twenty six of the 40 species were included in the region-wide phylogeny of *Cyrtandra* to place them in their biogeographic context and we were able to conclude that *Cyrtandra* arrived on Sulawesi for the first time c. 8 ma and that the diversity present there is the result of at least seven colonisation events with most arrivals originating from the Philippines.

2. Producing a well-sampled phylogeny of *Cyrtandra* across the region allowed us to develop a strategy for tackling this large genus taxonomically in the future in the absence of a functional infrageneric system (Chapter Three). The poor morphological diagnosability of the six major clades discovered in the molecular phylogenetic analysis, resulting from the homoplasy of macromorphological characters, combined with some degree of floristic exchange between islands, suggested that a single approach, either based on geography, morphology or molecular data, will not be satisfactory for *Cyrtandra*. Therefore, an integrative method will be most successful, as demonstrated in other large genera (Särkinen et al., 2015; Moonlight et al., 2018; Lucas et al., 2018). We assessed the concept of phylogenetically informed revisions of restricted geographic areas by studying the *Cyrtandra* species of (i) Sulawesi and (ii) Borneo and found it to be a promising approach.

3. Molecular dating, ancestral range estimation and biogeographic stochastic mapping allowed us to examine the geo-temporal patterns and evolution of southeast Asian *Cyrtandra* (Chapter Four). The great diversity of *Cyrtandra* seen in the Malesian region results from a recent radiation, with most speciation taking place in the last five million years. Borneo was recovered as the most likely ancestral range of the genus, with the current distribution of species resulting from a west to east migration across Malesia that corresponds with island emergence and mountain building. Our investigation also indicated high levels of floristic exchange between the islands on the Sunda shelf and an important role for the Philippines as a stepping stone to Wallacea and New Guinea. These patterns of recent speciation and west to east migration with Borneo as the ancestral area underlie much of the plant diversity in Southeast Asia and form an emerging paradigm in Southeast Asian plant biogeography.

4. Some new observations on speciation dynamics for Southeast Asian *Cyrtandra* can be made from this study (Chapters Three and Four) including (i) the notable absence of hybridisation in this area compared to the Pacific*,* possibly due to the role of pre-zygotic barriers associated with high levels of floral divergence in sympatric populations in southeast Asia although these barriers are known to be permeable; (ii) a remarkably stable genome with no variation in chromosome numbers recorded across its distribution, including the Pacific. These two observations are in marked contrast to other large genera such as *Begonia, Inga* and *Solanum* where hybridisation and ploidy changes are common (Figueiredo et al., 2014; Rollo et al., 2016; Hughes et al., 2018; Särkinen et al., 2018).

Future work

We have increased our knowledge of diversity in *Cyrtandra* and have gained some preliminary insights into speciation dynamics. In addition to much needed taxonomic research, achieving greater knowledge in this latter area is an obvious next step for *Cyrtandra.*

The concept of phylogenetically informed revisions of restricted geographic areas will be adopted first on the two most diverse islands of Southeast Asia: Borneo and New Guinea. We now have a key to fourteen lineages on Borneo that will form the basis for studying the 200 plus species on that island in the future. Preliminary research on New Guinea suggests

that there are at least eight lineages there which can be morphologically defined to inform future taxonomic studies on that island (Bramley pers. comm.). Recent collaboration on the genus in the Philippines (Olivar et al., accepted) and the generation of large amounts of new molecular data from these islands gives the potential for this approach to be adopted here too.

Understanding to what degree the great diversity seen in *Cyrtandra* is the result of adaptive diversification in terms of phenotypic traits or ecological factors, as has been seen in other groups, will be key (Breitkopf et al., 2015; Donoghue & Sanderson, 2015; Roalson & Roberts, 2016; Lagomarsino et al., 2017). Interestingly, studies in two clades of the ecologically similar genus *Begonia* strongly diverges from those predicted by an adaptive model; the high levels of diversity having developed through geographic speciation and Brownian motion through niche space (Moonlight, 2017). Studies of niche evolution in *Cyrtandra,* following similar methods, will be useful to assess whether the ecologically similar genus *Cyrtandra* also follows this pattern.

More detailed analysis on the genomic architecture of species differences in *Cyrtandra* will be useful as, based on our current understanding, *Cyrtandra* displays a somewhat different genomic history to other species-rich groups. Studies of non-model groups with complex speciation stories are needed to fill the 'unexplored corner' of the speciation study spectrum of genomic level studies (Campbell et al., 2018) and *Cyrtandra* is an ideal candidate group for this.

Full insight into the diversification dynamics of *Cyrtandra* requires greater sampling across its distribution and the filling of significant geographic gaps in southeast Asia, such as Kalimantan, Maluku and the southern Philippines. Combining the dataset presented here with the complementary dataset from the Pacific (Johnson et al., 2017; 2019) is in progress and will be an essential first step to extend our understanding of evolution across the genus.

The greatest insights in to the evolutionary dynamics of diversification are predicted to come from studies of clades of c. 500 to 1000 (Hughes et al., 2015) where 'dense sampling, both for interspecific and intraspecific diversity, detailed trait and geographical datasets, and adequate statistical power, are achievable'. We are better placed in *Cyrtandra* now to

achieve this aim with much expanded data sets and sampling from the centre of diversity of this genus in southeast Asia.

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Appendix 1: License information for inclusion of published papers and illustrations and declarations of author contributions.

Appendix 2

Atkins, H.J., Bramley, G.L.C., Johnson, M.A., Kartonegoro, A., Nishii, K., Kokubugata, G., Möller, M. & Hughes, M. 2020. A molecular phylogeny of Southeast Asian *Cyrtandra* (Gesneriaceae) supports an emerging paradigm for Malesian plant biogeography. *Frontiers of Biogeography* https://doi.org/10.21425/F5FBG44184

Appendix 3

Atkins, H.J., Heatubun, C.D., Galloway, L. & Bramley, G.L.C. 2019. Two new species, *Cyrtandra bungahijau* and *C. vittata,* and notes on *Cyrtandra* (Gesneriaceae) from Yapen Island, Indonesia. *Kew Bulletin* 74: 29 https://doi.org/10.1007/s12225-019-9817-2

Appendix 4

Nishii, K., Kokubugata, G., Möller, M. & Atkins, H.J. 2019. Notes on *Cyrtandra* (Gesneriaceae) from Japan, Taiwan and Batan Island (Philippines). *Edinburgh Journal of Botany* 76(3): 333-344.

Appendix 5

Kartonegoro, A., Bone, R. & Atkins, H.J. 2018. Eleven new species of *Cyrtandra* (Gesneriaceae) from Sulawesi, Indonesia. *Edinburgh Journal of Botany* 75(2):173-204

Illustrations included in Chapter Two:

Atkins, H.J. 2004. The *Gesneriacae* of Sulawesi II: seven new species of *Cyrtandra Edinburgh Journal of Botany* 60: 305–321.

Bone, R.E. & Atkins, H.J. 2013. Four new species of *Cyrtandra* (Gesneriaceae) from the Latimojong Mountains, South Sulawesi. *Edinburgh Journal of Botany* 70(3): 455-468.

Kartonegoro, A., Bone, R. & Atkins, H.J. 2018. Eleven new species of *Cyrtandra* (Gesneriaceae) from Sulawesi, Indonesia. *Edinburgh Journal of Botany* 75(2):173-204

Declarations relating to work included in the thesis where multiple authors are cited:

Chapter Two was conceived and written by HA. All of the figures and conservation assessments were produced by HA. Some of the taxonomic decision making was undertaken jointly with AK, especially relating to new species, some of which were published separately (see Appendix Four).

Chapter Three was conceived by HA. HA generated approximately two fifths of the molecular sequence data; scored all of the morphological data; carried out all of the analyses; prepared the figures and wrote the text. Other authors contributed molecular data, determinations and advice on morphological scoring and structure.

Chapter Four was conceived by HA and MH. HA generated approximately two fifths of the molecular sequence data; carried out all of the analyses, created the figures and wrote the text. Other authors contributed molecular data, determinations and advice on analyses.

Declarations relating to published work:

The work presented as Appendix One was published in *Frontiers of Biogeography* as 'A molecular phylogeny of Southeast Asian *Cyrtandra* (Gesneriaceae) supports an emerging paradigm for Malesian plant biogeography' by **Atkins, H.J**., Bramley, G.L.C., Johnson, M.A., Kartonegoro, A., Nishii, K., Kokubugata, G., Möller, M. & **Hughes, M**. This study was conceived by HA and MH. HA generated approximately two fifths of the molecular sequence data; carried out all of the analyses and created the figures. All authors contributed to the writing.

The work presented in Appendix Two was published in *Kew Bulletin* as 'Two new species, *Cyrtanrda bungahijau* and *C. vittata*, and notes on *Cyrtandra* (Gesneriaceae) from Yapen Island, Indonesia' by **Atkins, H.J**., Heatubun, C.D., Galloway, L. & Bramley, G.L.C. This study was conceived by HA. The taxonomic decision making was undertaken jointly by HA and GB. HA prepared all of the figures. All authors contributed to the writing.

The work presented in Appendix Three was published in *Edinburgh Journal of Botany* as 'Notes on *Cyrtandra* (Gesneriaceae) from Japan, Taiwan and Batan Island (Philippines)' by Nishii, K., Kokubugata, G., Möller, M. & **Atkins, H.J.** This study was conceived by all of the authors and all of the authors contributed to the writing. HA ran the analyses and prepared the figures.

The work presented in Appendix Four was published in *Edinburgh Journal of Botany* as 'Eleven new species of *Cyrtandra* (Gesneriaceae) from Sulawesi, Indonesia' by Kartonegoro, A., Bone, R.E. & **Atkins, H.J.** This study was conceived by HA and AK. Taxonomic decision making and writing were undertaken jointly. HA prepared all of the figures.

Appendix 2: Atkins, H.J., Bramley, G.L.C., Johnson, M.A., Kartonegoro, A., Nishii, K., Kokubugata, G., Möller, M. & Hughes, M. 2020. A molecular phylogeny of Southeast Asian *Cyrtandra* (Gesneriaceae) supports an emerging paradigm for Malesian plant biogeography. *Frontiers of Biogeography* 12(1): https://doi.org/10.21425/F5FBG44184

Frontiers of Biogeography 2020, 12.1, e44814

ReseaRch aRticle

Frontiers of Biogeography
the scientific journal of
the International Biogeography Society

A molecular phylogeny of Southeast Asian *Cyrtandra* (Gesneriaceae) supports an emerging paradigm for Malesian plant biogeography

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Abstract

The islands of Southeast Asia comprise one of the most geologically and biogeographically complex areas in the world and are a centre of exceptional floristic diversity, harbouring 45,000 species of flowering plants. *Cyrtandra*, with over 800 species of herbs and shrubs, is the largest genus in the family Gesneriaceae and is one of the most emblematic and species- rich genera of the Malesian rainforest understorey. The high number of species and tendency to narrow endemism make *Cyrtandra* an ideal genus for examining biogeographic patterns. We sampled 128 *Cyrtandra* taxa from key localities across Southeast Asia to evaluate the geo- temporal patterns and evolutionary dynamics of this clade. One nuclear and four chloroplast regions were used for phylogenetic reconstruction, molecular dating, and ancestral range estimation. Results from the dating analysis suggest that the great diversity of *Cyrtandra* seen in the Malesian region results from a recent radiation, with most speciation taking place in the last five million years. Borneo was recovered as the most likely ancestral range of the genus, with the current distribution of species resulting from a west to east migration across Malesia that corresponds with island emergence and mountain building. Lastly, our investigation into the biogeographic history of the genus indicates high levels of floristic exchange between the islands on the Sunda shelf and the important role of the Philippines as a stepping stone to Wallacea and New Guinea. These patterns underlie much of the plant diversity in the region and form an emerging paradigm

Highlights

- This paper provides the first well sampled phylogeny of *Cyrtandra* across Southeast Asia.
- One of the richest genera of the Asian rainforest understory, *Cyrtandra* appears to have originated in Borneo, and undergone west- to- east dispersal into the Pacific.
- Support was found for a mid- Miocene origin, with most extant diversity arising by speciation within the last 5 Ma.
- The Philippines appear to represent an important secondary source area and stepping stone to Wallacea, Taiwan and Japan, and New Guinea.
- *Cyrtandra* fits into an emerging paradigm for Southeast Asian plant geography, illustrating the role of geo- tectonic and climate processes in historical biogeographical patterns in the region.

Keywords: ancestral range estimation, biogeographic stochastic mapping, *Cyrtandra,* floristic exchange, island biogeography, molecular dating, recent divergence, Sahul shelf, Sunda shelf, Wallacea

Introduction

The islands of Southeast Asia comprise one of the most geologically and biogeographically complex areas in the world (Hall 2002, Lohman et al. 2011) and are the meeting and mixing point of floras and faunas of diverse origins (van Welzen et al. 2011, Richardson et al. 2012). The area is estimated to harbour approximately 45,000 species of vascular plants (Johns 1995) on more than 20,000 islands (Lohman et al. 2011). It contains the biodiversity hotspots of Sundaland, Wallacea and the Philippines (Brooks et al. 2006), and the mega- diverse island of New Guinea (Mittermeier et al. 2003, Takeuchi 2005, Hoover et al. 2017).

The Malesian region is a complex and intricate mosaic of islands of different origins with a dynamic history over the last 50 million years (Ma) (Hall 2002, 2012a,b). In the west of the region are the continental Sunda shelf islands of Sumatra, Java and Borneo, separated by shallow seas. In the centre are the numerous smaller terranes and oceanic islands that comprise the Philippines and Wallacea, and in the east is the Sahul shelf and the large island of New Guinea, which is itself of composite origin. Adding a layer of complexity to this is the changing climate of the past 50 ma (Morley 2012, 2018), most strikingly the fluctuating glacials and interglacials of the Pleistocene (Woodruff 2010, Morley 2012), which impacted sea levels and the extent of vegetation types (Woodruff 2010, Cannon 2012, Morley 2012).

Over the last decade, a number of dated molecular phylogenies (Thomas et al. 2012, Grudinski et al. 2014, Hughes et al. 2015, Williams et al. 2017) and meta- analyses (van Welzen et al. 2011, De Bruyn et al. 2014, Cray net al. 2015) have supplemented our knowledge of how current patterns of diversity have been shaped by the geological and climatic history of Malesia. These studies have provided insights into where and when lineages diversified and revealed some remarkable cross- taxon biogeographic patterns (Lohman et al. 2011), including the predominance of west- to- east dispersal patterns (Su and Saunders 2009, Baker and Couvreur 2012, Richardson et al. 2012, Thomas et al. 2012, Grudinski et al. 2014, Richardson et al. 2014, Crayn et al. 2015) and the identification of Borneo as an ancestral area and centre of diversity. Our current understanding of the biogeographic history of Malesia, however, remains incomplete and there is a need for additional well sampled phylogenies of taxa with distributions across the region (Richardson et al. 2012, Webb and Ree 2012).

Cyrtandra is the largest genus in the Gesneriaceae, with over 800 species of herbs and shrubs (Atkins et al. 2013) and is a key component of the herbaceous layer of Malesian rainforest found from sea level to 3000m (Burtt 2001, Atkins et al. 2013). Centres of diversity for the genus in Southeast Asia are Borneo (~200 spp.), the Philippines (~150 spp.), and New Guinea (~120 spp.) (Atkins et al. 2013). Its high species diversity, large number of narrow endemic species, and wide distribution make it an ideal genus for examining biogeographic patterns (Atkins et al. 2001, Cronk et al. 2005, Clark et al. 2008, Johnson et al. 2017) and investigating the processes which underlie current patterns of biodiversity (Bramley et al. 2004a, Johnson et al. 2015, 2019). The genus is characterised by a combination of two fertile stamens and an indehiscent fruit, which varies from a tough- walled green or brown capsule in the west to a fleshy berry that ripens white or rarely orange in the east of its distribution, particularly in New Guinea and the Pacific (Fig. 1) (Clark et al. 2013, Johnson 2017, Atkins et al.

Figure 1. Range of fruit morphology in SE Asian and Pacific *Cyrtandra*. a *C. pendula* (Sumatra) SUBOE 2; b *C.* sp (Sumatra) SUBOE 6; c *C.* sp (Sumatra) SUBOE 9; d *C.* sp (New Guinea) Briggs MB838; e *C. pogonantha* (Samoa) Wood 16941 f *C. celebica* (Sulawesi) BAKK 12; g *C. polyneura* (Sulawesi) BAKK 18; h *C. pulleana* (New Guinea) Briggs MB845; I *C. richii* (Samoa) Wood 16935. Photos: a- c, f & g: Sadie Barber, e & i: Melissa Johnson, d & h: Marie Briggs.

2019). The flowers are often white but species with pink, red, purple, yellow, green, and orange flowers are also known (Fig. 2).

Earlier phylogenetic studies of Southeast Asian *Cyrtandra* have focused on particular localities with dense sampling from a small number of locations (Atkins et al. 2001, Bramley et al. 2004a). Larger scale studies have focused on *Cyrtandra* diversification across the Pacific (Cronk et al. 2005, Clark et al. 2008, 2009, Johnson et al. 2017), and these studies have signalled that the origin of the genus is within the Malesian region. Here, we sample *Cyrtandra* taxa from key localities across Southeast Asia to construct a well-resolved phylogenetic tree based on one nuclear and four chloroplast regions. We use this to estimate divergence times, ancestral ranges, and dispersal patterns in order to gain insights into the evolutionary history of *Cyrtandra.* We then consider whether the key patterns recovered for other taxa in Southeast Asia are also seen in *Cyrtandra,* one of the most species-rich and emblematic genera of the Malesian rainforest understorey.

Methods

Taxon sampling

We sampled a total of 192 accessions representing 128 *Cyrtandra* taxa (Supplementary Table S1), including samples that were representative of all the key regions in Southeast Asia (Fig. 3). Table 1 gives a summary of our sampling against current estimates of species numbers by island for the Southeast Asian region (Atkins et al. 2013). Five taxa from within Didymocarpinae (the same subtribe as *Cyrtandra*) were selected as outgroups (*Aeschynanthus roseoflorus, A. buxifolius, Agalmyla chalmersii, Didymocarpus antirrhinoides,* and *Loxostigma griffithii*). Outgroups were selected to reflect those in recent molecular dating analyses (Johnson et al. 2017, Ranasinghe 2017) to facilitate dating of the nodes using secondary calibration points. We applied names to as many of the samples as possible but many of the samples represent undescribed diversity. There is no single taxonomic treatment for *Cyrtandra* and therefore species concepts and identifications follow those used in regional treatments (e.g., Atkins and Cronk, 2001, Bramley et al. 2004b).

Molecular methods

DNA extraction methods and PCR conditions followed Nishii et al. (2019). Details of the primers used for each of the five regions (ITS, *mat*K, *trn*L-F, *psb*A-*trn*H and *rpl*32-*trn*L) are given in Table 2. Chloroplast sequence data (*mat*K, *trn*L-F, *psb*A-*trn*H and *rpl*32-*trn*L) from two of the outgroup collections, *Agalmyla chalmersii* and *Didymocarpus antirrhinoides,* was gifted to the project by Prof Gao Lian Ming, Kunming Institute of Botany, Chinese Academy of Sciences, Yunnan, China.

Phylogenetic analyses

Maximum Parsimony (MP) analyses were initially conducted on individual regions to visually assess

Figure 2. Range of flower morphology in SE Asian *Cyrtandra*. a *Cyrtandra rantemarioensis* (Sulawesi) RBGE living collections 20000622; b. *Cyrtandra luteiflora* (Sulawesi) RBGE living collections 20021194; c. *Cyrtandra purpureofucata* (Sulawesi) Thomas & Ardi 09-88; d. *Cyrtandra serratifolia* (Sulawesi) RBGE living collections 20021210; e. *Cyrtandra celebica* (Sulawesi) BAKK 15; f. *Cyrtandra mollis* (Sulawesi) BAKK 42; g. *Cyrtandra cleopatrae* (Palawan, Philippines) RBGE living collections 19981745; h. *Cyrtandra bungahijau* (Yapen Island, New Guinea) RBGE living collections 20090826; i. *Cyrtandra peltata* (Sumatra) RBGE living collection 20161282; j. *Cyrtandra vittata* (Yapen Island, New Guinea) RBGE living collection 20090734. Photos: a & b: Steve Scott. c: Wisnu Ardi. d & g: Hannah Atkins. e, f & i: Sadie Barber. j: Lynsey Wilson

congruence, with areas of conflict determined by examining the placement of individual taxa on each gene tree. Relationships were considered incongruent if the placement of taxa varied among the individual gene trees and exhibited MP- BS values > 80%. MP analyses were carried out using PAUP v 4.0a163 (Swofford 2002) on unweighted and unordered characters. Alignment gaps were treated as missing data. A heuristic search was carried out using stepwise random addition of 10,000 replicates, with TBR and Multrees on. Statistical

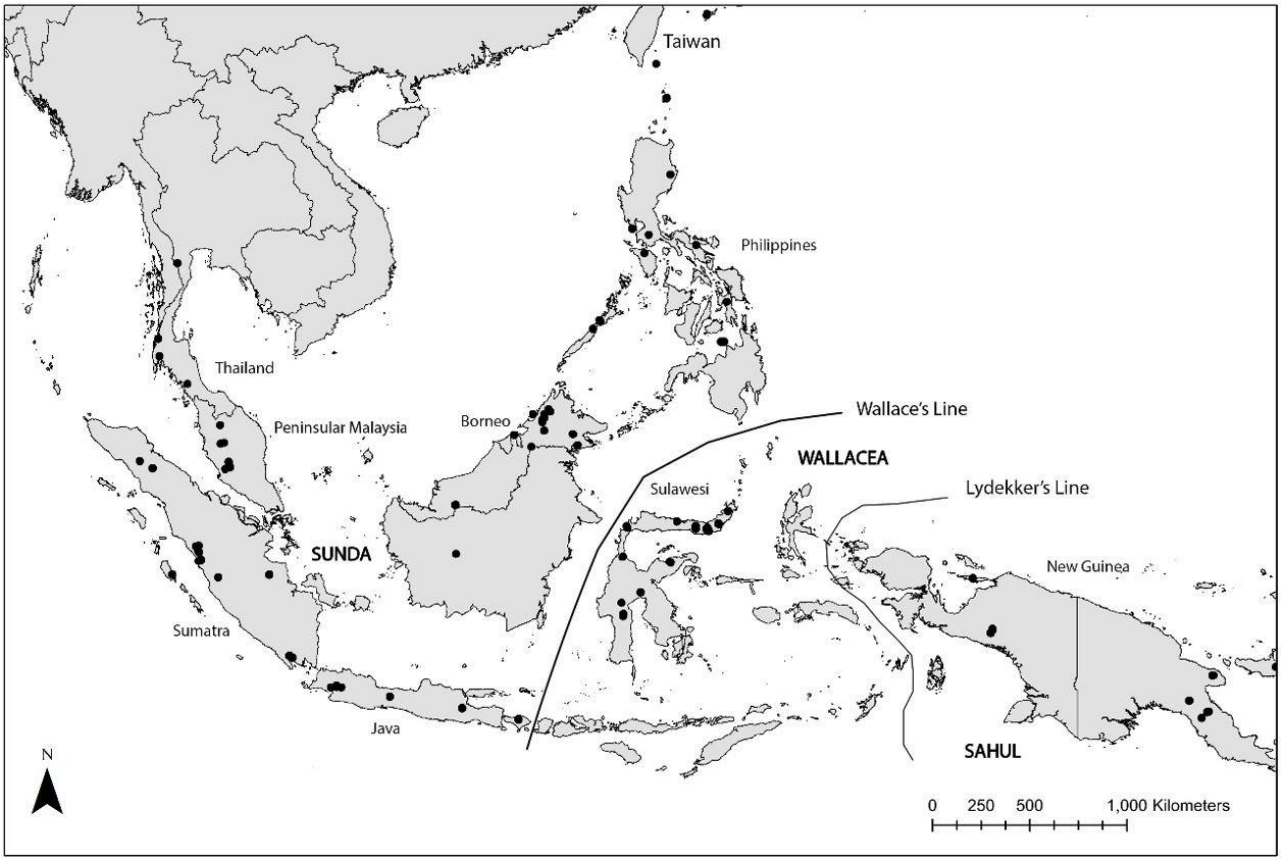


Figure 3. Map showing collection locations of southeast Asian *Cyrtandra* samples included in the present study. Pacific islands not shown on map.

Table 1. Current estimates of species numbers in *Cyrtandra* by area across Malesia, the number of species included in the present study, and the percentage of the total that this represents.

Geographic region (Southeast Asia only)	Total number of species (following Atkins et al. 2013)	Number of species sampled	% sampled (based on maximum numbers where ranges given in Atkins et al. 2013)
Thailand	6	2	33
Peninsular Malaysia	9	5	56
Sumatra	40- 44	27	61
Java	19- 32	11	34
Lesser Sunda Islands	3	1	33
Borneo	181- 200	26	13
Taiwan and Japan	2	2	100
Philippines	105- 150	17	11
Sulawesi	22- 40	26	65
Moluccas	3	0	0
Australia	1	1	100
New Guinea	107- 120	10	8

branch support was obtained from 10,000 heuristic bootstrap replicates each starting with a random addition tree, optimised with TBR on and Multrees off. For Bayesian Inference and Maximum Likelihood analyses, the data were divided into seven partitions (ITS spacers, 5.8S gene, *psbA-trnH*, *rpl*32- *trn*L, *trn*L-F, *matK* coding region, *matK* intron region) and analysed under the best-fit model of nucleotide evolution for each genic region selected using the AIC criterion as implemented in MrModeltest v 2.4 (Nylander 2004) (GTR+G for ITS spacers, *trn*L-F, *psbA-trnH* and *matK* intron region, GTR+I+G for *rpl*32-*trn*L and *matK* coding region and SYM+I for the ITS 5.8S gene). Bayesian inference (BI) phylogenetic analyses were carried out using Mr Bayes v 3.2.6 (Ronquist et al. 2012) on the partitioned dataset. Two runs with four chains each were implemented, run for 10,000,000 generations with a tree sampled every 1000th generation. The first 10% of sampled trees were discarded as burn-in and the remainder summarised as a maximum clade credibility tree and posterior probabilities (PP) extracted. Maximum Likelihood (ML) analyses were conducted with RAxML v 8 (Stamatakis 2014) via the CIPRES Gateway (Miller et al. 2010). The search for the optimal ML tree was performed with the 'Let RAxML halt bootstrapping automatically' parameter selected. For the ML and BI analyses, tree topology and node support were examined in FigTree v. 1.4.3 (Rambaut 2007).

Divergence time estimates

A time-calibrated phylogeny was constructed on the partitioned five-gene dataset using an uncorrelated relaxed lognormal clock in the program BEAST v. 1.10.1 (Drummond et al. 2012, Rambaut et al. 2018). Secondary age calibrations were necessary as there are no unambiguous fossils in the Gesneriaceae family (Wiehler 1983, Clark et al. 2008). Five calibration points were taken from the family-wide phylogeny in Ranasinghe (2017) (Table 3) and were assigned a lognormal prior following Ho and Phillips (2009) and Schenk (2016) . Five separate runs were carried out, beginning with a random tree and run for 100 million generations under a Yule model of speciation, sampled every 1000 generations. Following Condamine et al. (2015) sensitivity analyses using the Birth-Death tree prior were also run and the results were not significantly changed by choice of tree prior. The results from the

Table 2. Details of primers used for PCR and sequencing of the five gene regions for *Cyrtandra*.

Region	Name	Direction	Primer sequences	References
ITS	ITS_5P	Forward	GGA AGG AGA AGT CGT AAC AAG	Möller & Cronk 1997
ITS	ITS_8P	Reverse	CAC GCT TCT CCA GAC TAC A	Möller & Cronk 1997
*trn*LF	trnLcG	Forward	GTG AAG ACT TCT AAA TTC AGA GAA AC	Nishii et al. 2019
*trn*LF	trnLf	Reverse	ATT TGA ACT GGT GAC ACG AG	Taberlet et al. 1991
*psb*A-*trn*H	psbAf	Forward	GTT ATG CAT GAA CGT AAT GCT C	Sang et al. 1997
*psb*A-*trn*H	trnHr	Reverse	CGC GCA TGG TGG ATT CAC AAA TC	Sang et al. 1997
*rpl*32-*trn*L	rpl32-F	Forward	CAG TTC CAA AAA AAC GTA CTT C	Shaw et al. 2007
*rpl*32-*trn*L	$trnL^{(UAG)}$	Reverse	CTG CTT CCT AAG AGC AGC GT	Shaw et al. 2007
*mat*K	matK.206F	Forward	CCG GGT TAT GAC AAT AAA TCC AGT	Luna et al. 2019
*mat*K	matK.946R	Reverse	ATA AAT CCT TCT TGG ATG AAA CCA C	Luna et al. 2019
*mat*K	matK.cy2F	Forward	TGG CAA TGG CAT TTT TCG CT	Nishii et al. 2019
*mat*K	matK.1734R	Reverse	CCG TGC TTG CAT TTT TCA TTG C	Luna et al. 2019

Table 3. Details of the five secondary calibration points (node age, standard deviation, and prior distribution) from Ranasinghe (2017) used to generate the dated phylogeny of *Cyrtandra* in BEAST.

Calibration point	Node	Node Age (Ma)	Prior distribution	Standard deviation
1	Internal *Cyrtandra* node	6.42	LogNormal	2.0 (2.5, 10.97)
2	*Loxostigma* and *Cyrtandra* crown	18.03	LogNormal	2.0 (14.18, 21.85)
3	*Aeschynanthus* and *Loxostigma/ Cyrtandra* crown	18.79	LogNormal	2.0 (14.89, 22.71)
4	*Billolivia* (and *Aeschynanthus/ Loxostigma/ Cyrtandra* crown	20.15	LogNormal	2.0 (16.18, 24.28)
5	*Agalmyla* (and *Billolivia/ Aeschynanthus/ Loxostigma/ Cyrtandra* crown)	20.99	LogNormal	2.0 (17.04, 25.14)

analysis with the Yule model are presented here. Plots of the logged parameters for each run were visualised using Tracer v. 1.7.1 (Drummond and Rambaut 2007) to confirm convergence between runs by examining log likelihood plots and ensuring that Effective Sample Size (ESS) values were above 200. The trees from each run were combined in Logcombiner v 1.10.1 (Drummond et al. 2012) and support values and tree statistics were summarised onto a single maximum clade credibility (MCC) tree using the programme TreeAnnotator v. 1.10.1 (Drummond et al. 2012), visualised in FigTree v. 1.4.3 (Rambaut 2007).

Ancestral range estimation

The R package BioGeoBEARS (BioGeography with Bayesian Evolutionary Analysis in R Scripts) (Matzke 2013, 2014) was used to estimate ancestral ranges for *Cyrtandra* under three historical biogeography methods: DEC (Dispersal- Extinction- Cladogenesis; Ree and Smith, 2008), DIVA (Dispersal- Vicariance Analysis; Ronquist 1997), and BayArea (Bayesian inference of historical biogeography for discrete areas; Landis et al. 2013) models. Descriptions of each of these models and how BioGeoBEARS replicates their key assumptions are given in Matzke (2013). To allow for model comparison, all the models were implemented in a maximum likelihood framework. As *Cyrtandra* is distributed across a system of islands and shows high levels of narrow endemism, founder event speciation was likely to be a highly relevant biogeographic process (Cowie and Holland 2006, Matzke 2013, Roalson and Roberts 2016, Johnson et al. 2017), so we also explored the influence of founder event speciation in the analysis by including '+J' versions of the models. Due to concerns about the statistical methods in the package, both in terms of how the best fit model is selected and how the +J parameter operates (Ree and Sanmartín 2018), results from all of the six models will be discussed. Given that sampling density can also impact the results, a summary of our sampling rates against current species estimates is presented in Table 1.

The MCC tree was pruned to include only a single representative of each species except for those species that have multi- island distributions and were not monophyletic, such as *C. pendula*. In these cases, we included one representative from each area (following Johnson et al. 2017, 2019). For monophyletic species with multi- island distributions, such as *C. umbellifera* from Taiwan and the Philippines and *C. sandei* from Java and Sumatra, only one sample was included, and these were coded as present in each respective area in the analysis. Each taxon was assigned a distribution using 13 geographic regions based on a combination of geological information (Hall 2002, 2012), previous biogeographical studies (Atkins et al. 2001, van Welzen et al. 2011, Hughes et al. 2015) and current knowledge of species distributions and relationships in *Cyrtandra* (Atkins and Cronk 2001, Bramley and Cronk 2003, Johnson et al. 2017, Kartonegoro et al. 2018). The 13 regions used were: Hawaii, Marquesas and Society Islands, Japan and Taiwan, Australia, Thailand, Peninsular Malaysia, Sumatra, Borneo, Sulawesi, New Guinea, Solomon Islands, Java and the Lesser Sunda Islands, and the Philippines.

The outgroup taxa were removed so as not to influence the root ancestral area. We set the maximum number of areas to two, as *Cyrtandra* is characterised by high levels of narrow endemism and only *C. pendula* is currently recognised as having a range size greater than two areas. The six models (DEC, DIVA- like, BayArea- like, and the '+J' variations of each) were compared for statistical fit using the Akaike Information Criterion (AIC) and a Likelihood Ratio Test (LRT).

Lastly, we used BioGeoBEARS to perform a Biogeographic Stochastic Mapping (BSM) analysis (Matzke 2016, Dupin et al. 2017). This generates simulated histories based on a given biogeographical model, the phylogeny, observed range data, and the calculated ancestral state probabilities at each node averaged over many realisations. The biogeographical events that are possible include within- area speciation, vicariance and dispersal events (range expansions and founder events). Event frequencies were estimated by taking the mean of event counts from 100 BSMs. We ran the BSM exercise on all the models to evaluate the impact that the choice of model has on the event counts.

Results

Phylogenetic relationships

In total, 940 new sequences were generated for this study and our final data matrix contained five gene regions and 5438 aligned base positions. Tree topologies of independent MP analyses of the ITS, *trn*L- f, *psb*A- *trn*H, *rpl*32, and *mat*K regions were congruent although there was far greater resolution in the ITS dataset than in any of the others individually. The tree based on the concatenated five- gene dataset (Fig. 4,5) largely followed the topology of the ITS tree, with increased support for the relationships between the major clades. There were no incongruences with greater than 80% MP bootstrap support. ML, MP, and BI analyses of the combined dataset resulted in trees with congruent topologies.

Divergence time estimates

In this study, divergence time estimates suggest that the genus *Cyrtandra* split from its closest relative, *Loxostigma,* c. 16 Ma (14.18- 18.34, 95% HPD) during the early Miocene (Fig. 6). The crown age of *Cyrtandra* is estimated to be 13 Ma (10.84- 15.56, 95% HPD). Summaries of estimated dates are shown in Table 4. Using mean ages, 109 of the 128 taxa included in the analysis split from their most recent ancestor in the last 5 ma (method following Madriñán et al. 2013; Richardson et al. 2014).

Ancestral range estimation

Significant improvement in the likelihood of the three standard models (DEC, DIVA- like, and BayArea- like) was seen when the founder event parameter (+J) was added (Table 5). Of the six models evaluated, the best fit model was BayArea- like +J.

Under all six models analysed, the island of Borneo was recovered as the most likely ancestral area for *Cyrtandra* (Fig. 7).

Biogeographic stochastic mapping

Under the best fit model, Borneo is resolved as a major source area with ~33% (11.5 events) of all dispersal events originating here (Fig. 8, Table 6). Dispersal from Borneo was most frequent to Sumatra (3.0 events) and the Philippines (2.7 events), followed by Peninsular Malaysia (2.0 events) and Sulawesi (1.5 events). In contrast, Borneo was the recipient of only 0.8% of dispersals from all other areas and no event counts from any single area above 0.1. The Philippines was the second largest source area with 21% of dispersal events originating here. The majority of dispersal events from the Philippines were to the island of Sulawesi (3.9 events), but there were also dispersals from the Philippines north to Taiwan and Japan (1.5 events) and east to New Guinea (0.9 events). The greatest source of dispersals into the Philippines was Borneo (2.7 events). Relatively high levels of dispersal were also recovered between Java, Sumatra, and Peninsular Malaysia (2.5 events from Sumatra to Peninsular Malaysia, 3.0 events from Java to Sumatra, and 1.2 events from Sumatra to Java). In marked contrast to Borneo, Sulawesi emerged as an island of high immigration (receiving 20% of all dispersals) and low emigration, with only 2% of dispersals originating here. New Guinea is resolved as the most likely source of dispersals to the Marquesas (0.9 events), Australia (1.0 event), and the Solomon Islands (1.0 event). The stochastic mapping exercise is more impacted by the choice of model than the ancestral range estimation as the six models rely on different biogeographic processes. In terms of dispersal patterns and potential routes through the region, however, Borneo is always in the top three sources of dispersal in all the models, along with the Philippines and Sumatra. Sulawesi is always interpreted as being a poor source of dispersals under all models. The Philippines is the most important source of dispersals north to Taiwan and Japan under all models. It is the highest source of dispersals south to Sulawesi in all but the two worst fit models where it is the second highest after Borneo; and it is the highest source of dispersals east to New Guinea in all but the two worst fit models where Sumatra, Sulawesi, or Borneo are interpreted as the most important source. New Guinea is the most likely source of dispersals to Australia, the Marquesas/ Society Islands, and the Solomon Islands under all models.

Discussion

Phylogenetic patterns and relationships

There was no incongruence between the nuclear and chloroplast datasets in our large Malesian sample and hence no detectable evidence of hybridisation. This is in marked contrast to previous phylogenetic studies of *Cyrtandra,* where extensive hybridisation and/or incomplete lineage sorting has been reported, principally in Hawaii (Pillon et al. 2013, Johnson et al. 2019) but also in the recent radiation of the genus in the Pacific (Johnson et al. 2017). This also differs from the ecologically and biogeographically similar genus *Begonia,* where the high prevalence of hybrid events is considered to be an important factor driving genomic change and species evolution (Hughes et al. 2018). A recent study of reproductive isolation in four species of Hawaiian *Cyrtandra* showed that boundaries between sympatric *Cyrtandra* species are maintained predominantly through postzygotic barriers (Johnson et al. 2015). In Hawaii, all 60 species are the result of a single dispersal event to the archipelago < 5 ma (Cronk et al. 2005, Clark et al. 2008, 2009, Johnson et al. 2017), and species are remarkably similar in floral morphology and ecological preference, such that hybridisation is

Table 4. Estimated ages (Ma) of major nodes (crown and stem age of *Cyrtandra*) in the present study using BEAST, and comparable nodes in earlier studies. Ranges in parentheses represent the 95% highest posterior density (HPD).

Node	Present study	Johnson et al. 2017	Roalson and Roberts 2016
Cyrtandra stem	16.3 (14.28- 18.43)	25.27 (16.9- 35.02)	30.45 (14.79- 37.54)
Cyrtandra crown	13.38 (11.05- 15.79)	17.29 (12.54- 22.15)	11.08 (3.25- 21.78)

Table 5. Results of biogeographical model testing in BioGeoBEARS for *Cyrtandra*. Model parameters include anagenetic dispersal (d), extinction (e), and jump dispersal or founder events (j). The best fit model of BayAreaLike+J is highlighted in bold.

Model	LnL	AIC	AIC_wt	# parameters	d	e	J
DEC	- 258.8	521.7	1.80E- 21	2	0.0055	0.014	0
DEC+J	- 216	438	0.0027	3	0.0012	1.00E- 12	0.013
DIVALIKE	- 252.4	508.7	1.20E- 18	2	0.0058	1.00E- 12	0
DIVALIKE+J	- 218.3	442.6	0.0003	3	0.0014	1.00E- 12	0.013
BAYAREALIKE	- 280.4	564.8	8.00E- 31	2	0.0059	0.092	0
BAYAREALIKE+J	**-210.1**	**426.2**	**1**	**3**	**0.0005**	**0.0043**	**0.013**

LnL = Log Likelihood, AIC = Akaike Information Criterion, AIC wt = AIC weight

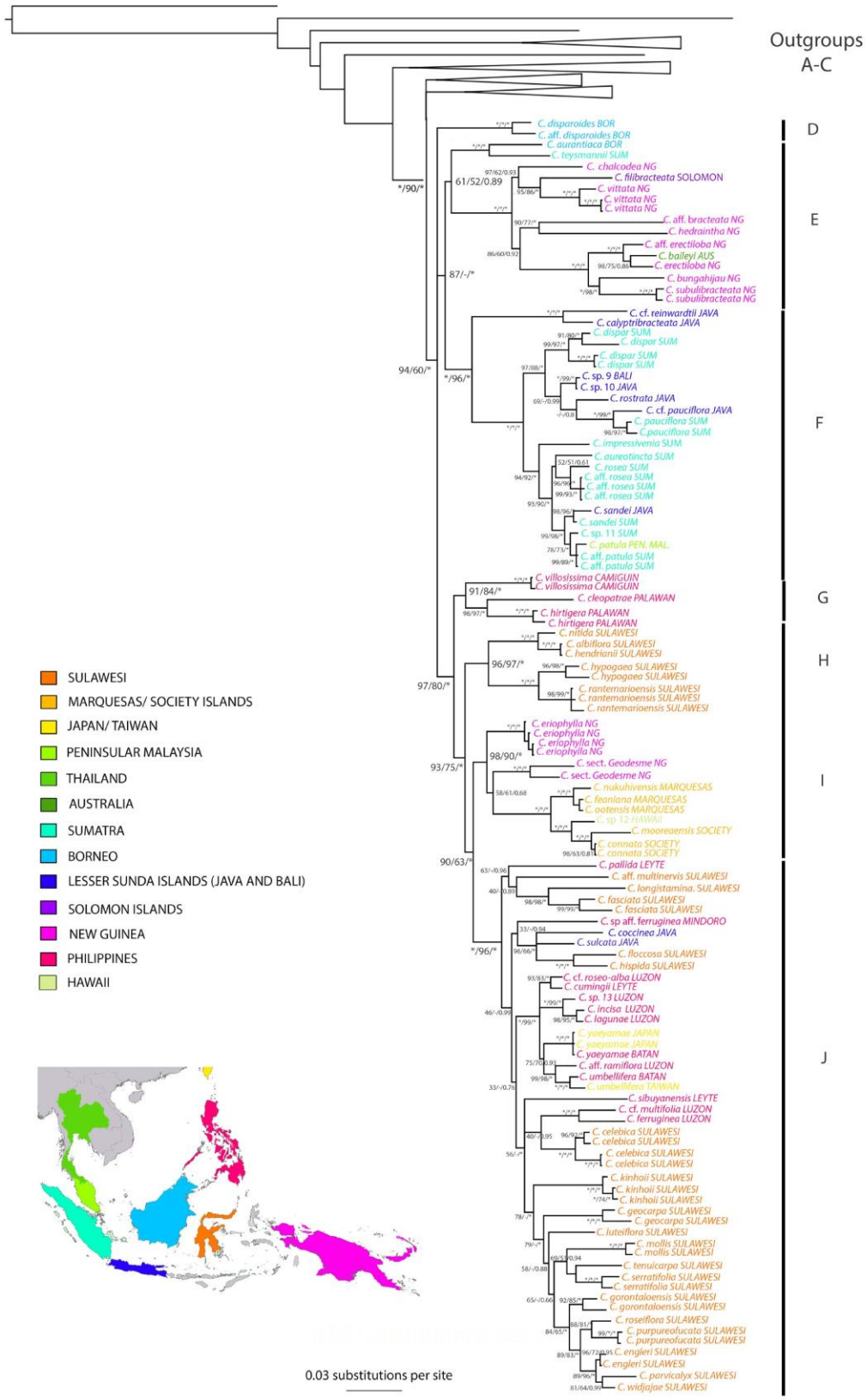
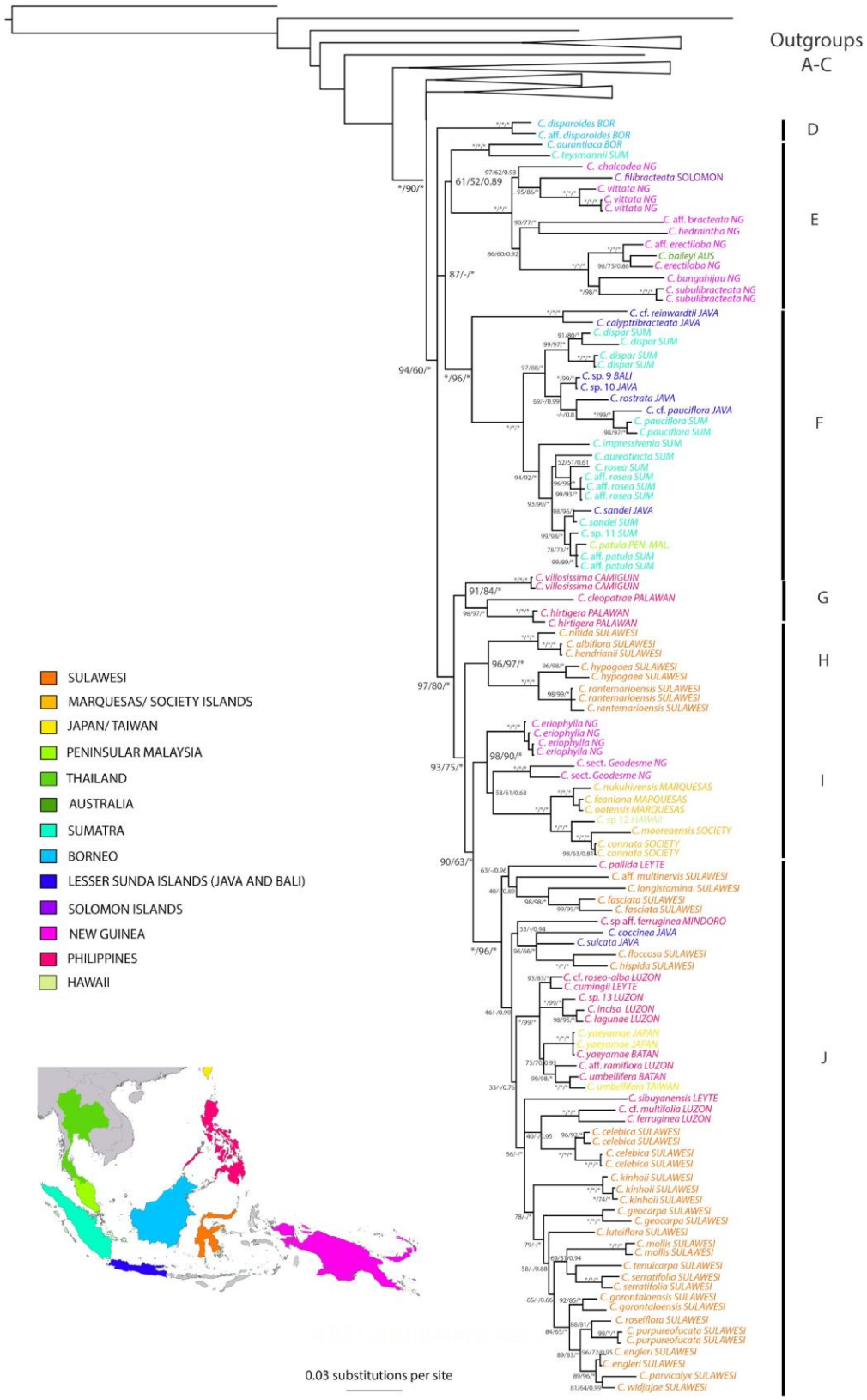


Figure 5. Bayesian inference tree of *Cyrtandra* based on the combined ITS, *psb*A-*trn*H, *rpl*32- *trn*L, *trn*L- F, and *mat*K regions, and highlighting clades D- J. Node support is indicated as Maximum Likelihood Bootstrap Support (ML- BS), Maximum Parsimony Bootstrap Support (MP- BS), and Bayesian Posterior Probabilities (BI- PP). Maximum values (100% BS or 1.0 PP) are indicated by *. No support (< 50% BS or 0.50 PP) is indicated by - . Species names are colour- coded by geographic region. Pacific islands not shown on map.



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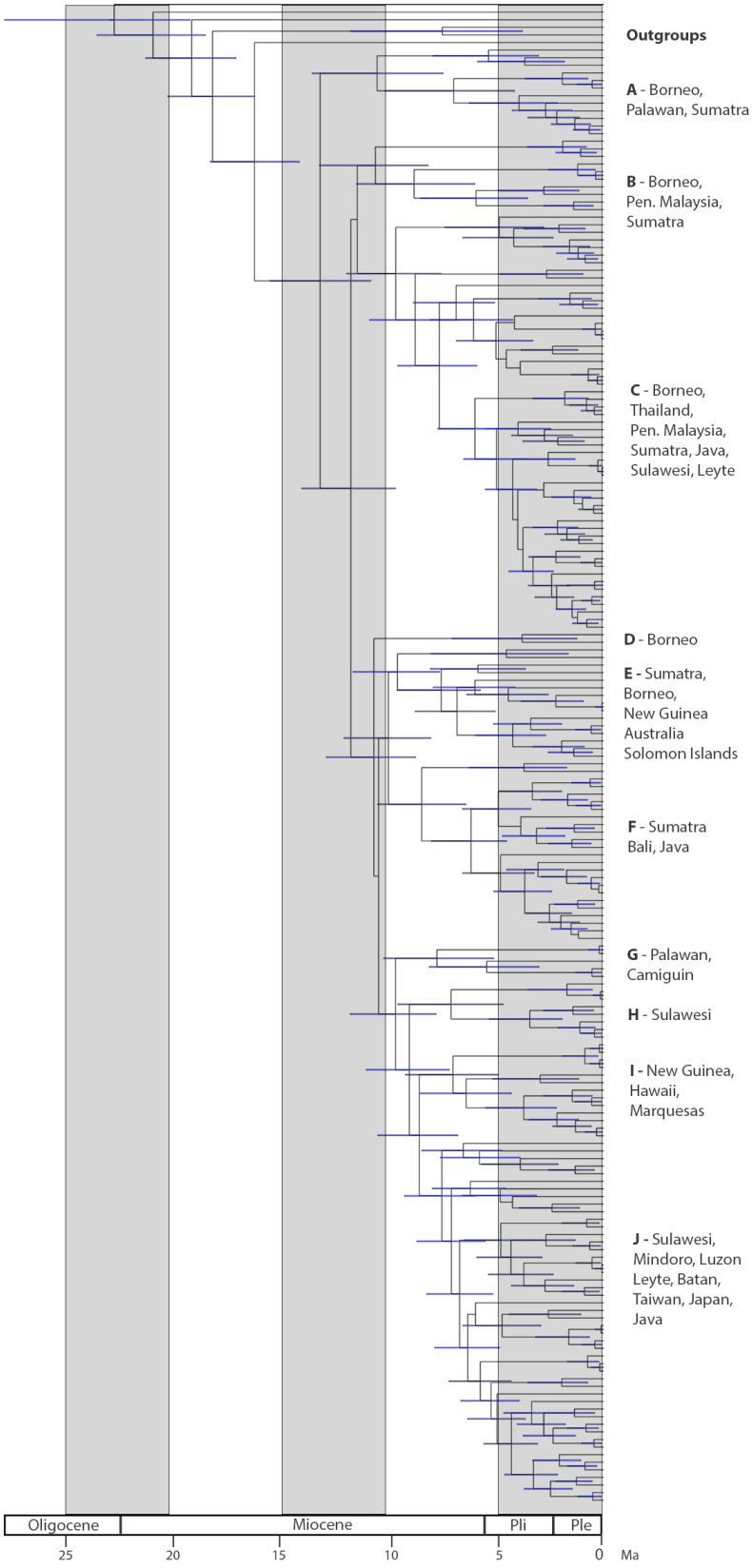

Figure 6. Maximum clade credibility tree of *Cyrtandra* based on a BEAST analysis of the combined ITS, *psb*A-*trn*H, *rpl*32- *trn*L, *trn*L- F, and *mat*K regions. Mean divergence time estimates are shown as millions of years ago (Ma), with the blue boxes showing the 95% highest posterior density (HPD). Pliocene is abbreviated to Pli and Pleistocene to Ple in the Time Scale below the tree.

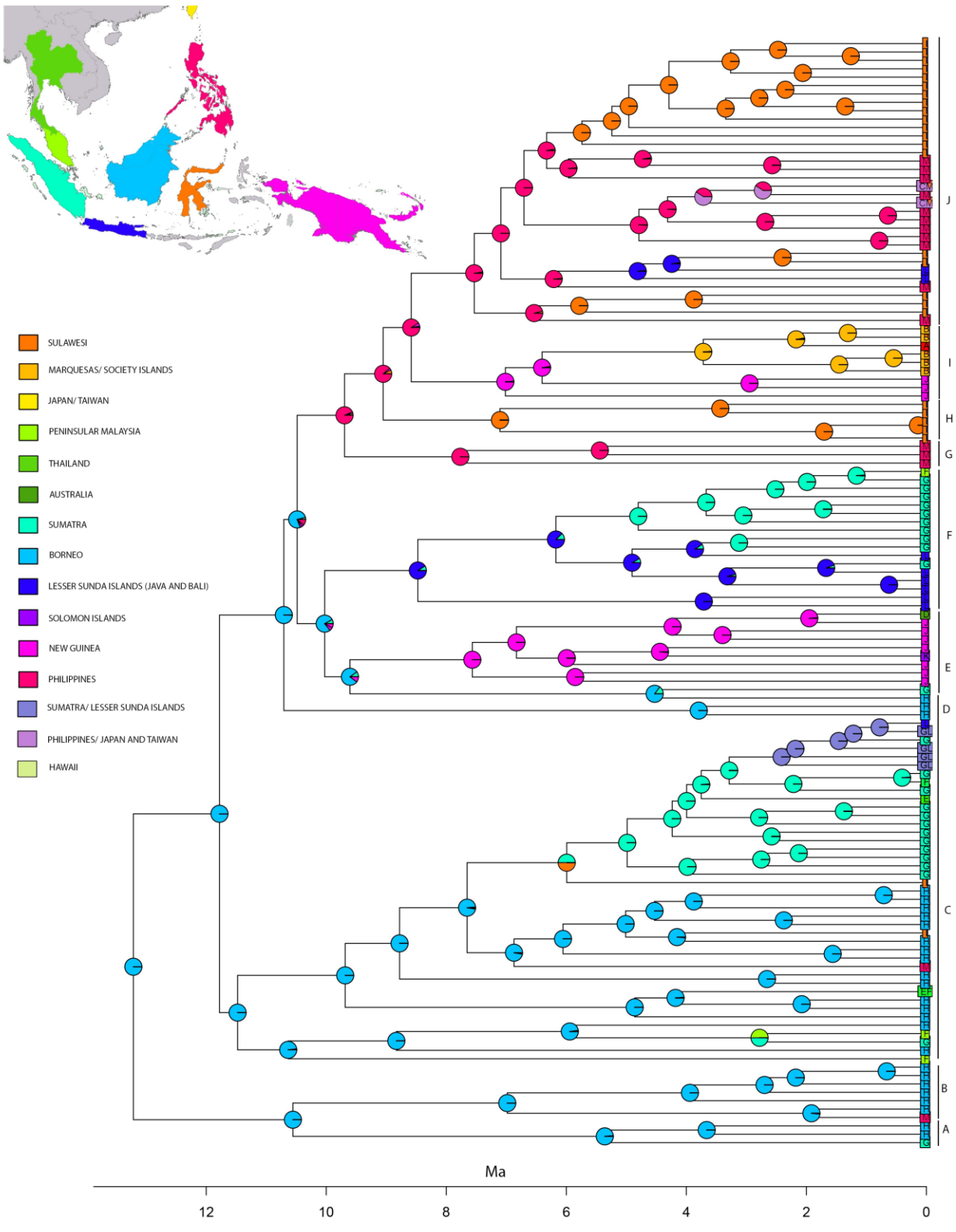

Figure 7. Ancestral range estimation for *Cyrtandra* based on the ultrametric tree produced in BEAST, and the best model determined by BioGeoBEARS (BayArea- like +J). Areas are colour- coded for the 13 geographic regions used in the analysis. Pacific islands not shown on map. Pie graphs at each node indicate the probability of a given area (or combined areas).

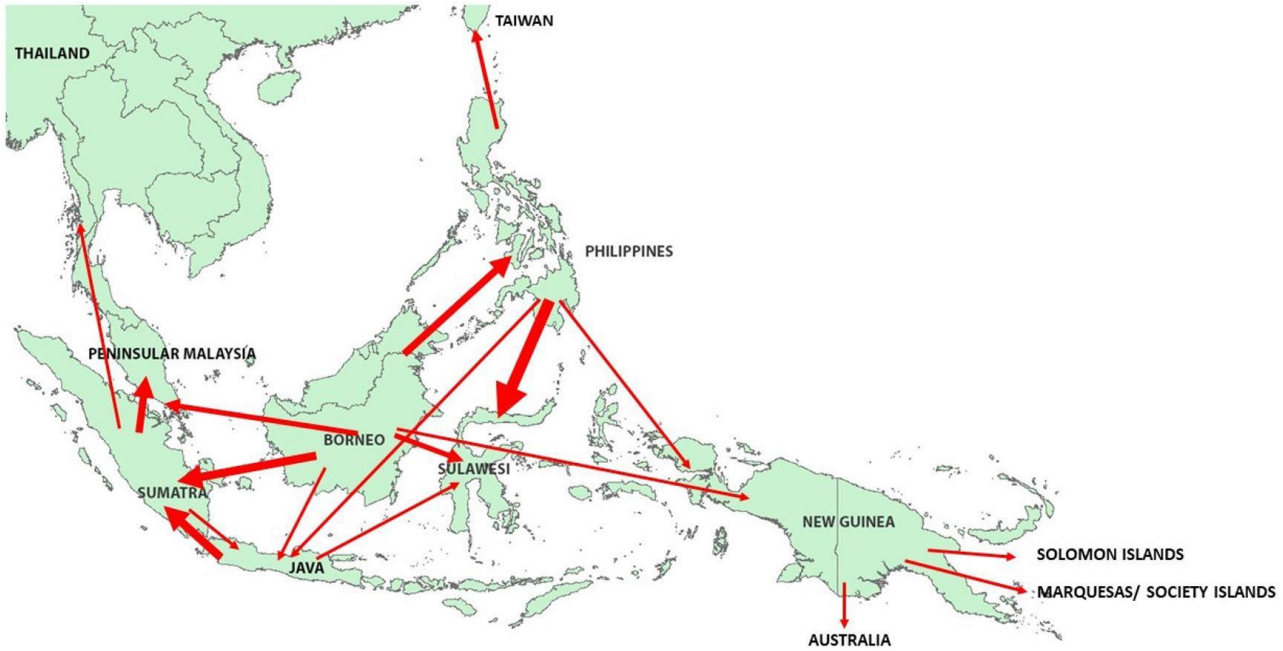

Figure 8. Summary of dispersal events in *Cyrtandra* estimated using a Biogeographic Stochastic Mapping (BSM) analysis in BioGeoBEARS based on the best fit model of BayArea+J (full results given in Table 6). The weight of each line indicates the number of predicted dispersal events (both founder and range expansion). All event counts of 0.9 and above are included.

Table 6. Summary of all dispersal counts for *Cyrtandra* averaged across 100 BSMs in BioGeoBEARS. Mapping was performed using parameters from the best- fit model of BayArea- like+J. Colour temperature indicates the frequency of events, with warmer colours indicating more common events (Red = >2.9, Orange = 2.0- 2.9, Yellow = 0.9- 1.9, Green = < 0.9). The ancestral states (i.e., where the lineage dispersed from) are given in the row, and the descendant states (where the lineage dispersed to) are given in the column.

	TO	A	B	C	D	E	F	G	H	I	J	K	L	M		
FROM		Hawaii	Marquesa/SI	Japan/Taiwan	Australia	Thailand	P. Malaysia	Sumatra	Borneo	Sulawesi	New Guinea	Solomon	Java/Bal	Philippines	TOTALS	As %
A	Hawaii	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0.1	0.3
B	Marquesas/ Society Is	1.0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	2.8
C	Japan/ Taiwan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D	Australia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E	Thailand	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0.5	1.4
F	Pen. Malaysia	0	0	0	0	0.5	0	0.5	0	0	0	0	0	0	1.0	2.8
G	Sumatra	0	0	0	0	1.0	2.5	0	0.1	0.	0.1	0	1.2	0	5.4	15.3
H	Borneo	0	0	0	0	0.5	2.0	3.0	0	1.	0.9	0	0.9	2.7	11.5	32.7
I	Sulawesi	0	0	0	0	0	0	0.5	0	0	0	0	0	0.2	0.7	2.0
J	New Guinea	0	0.9	0	1	0	0	0	0.1	0.1	0	1	0.1	0.2	3.4	9.7
K	Solomon Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L	Java and Bali	0	0	0	0	0	0	3.0	0	1.0	0.1	0	0	0.1	4.2	11.9
M	Philippines	0	0	1.5	0	0	0	0	0.1	3.9	0.9	0	1	0	7.4	21.0
TOTALS		1	1	1.5	1	2	5	7	0.3	7	2	1	3.2	3.3	35.3	
As %		2.8	2.8	4.2	2.8	5.7	14	20	0.8	20	5.7	2.8	9.1	9.3		100

widespread. In contrast, sympatric Malesian *Cyrtandra* are more likely to be from distantly related lineages (Bramley et al. 2004a), and this is reflected by the higher level of floral divergence (Fig. 2) and apparent lack of hybridisation amongst sympatric species, all of which is congruent with pre- zygotic barriers playing a large role in maintaining species boundaries.

The majority of the 36 named taxa that were represented by more than one sample resolved as monophyletic with strong support, including two species with multi- island distributions, *C. umbellifera* from Taiwan and the northern Philippines (Clade J, Fig. 5) and *C. sandei* from Java and Sumatra (Clade F, Fig. 5). There were four cases where morphologically similar species pairs resolve as paraphyletic with respect to each other, such as the red- flowered *C. clarkei* and *C. kermesina* from Sabah (Clade B, Fig. 4). We might expect to see examples such as this in a recently evolved group where weak gene flow may be a barrier to regaining monophyly following speciation, as has been recorded elsewhere in Gesneriaceae (Hughes et al. 2005). The most striking examples of polyphyly are seen in the widespread and morphologically variable *C. pendula* and *C. picta,* distributed across a number of islands. Given patterns elsewhere in the genus, it seems likely that these species names do not represent natural groups but rather a phenetic assemblage which will need to be addressed through further collecting and revisionary work.

Cyrtandra species in New Guinea appear to have much wider distributions than are typically found elsewhere in Malesia (Atkins et al. 2019). This may indicate a shift in dispersal ability as so many of the New Guinea species have fleshy fruits. Alternatively, this may signal that these taxa represent very recent radiations that have not yet been subjected to range contractions or extinction.

Divergence times

The origin and early diversification of *Cyrtandra* in the region dates to the mid Miocene (crown age 13 Ma), and most of the current diversity in Southeast Asia is the result of speciation in the last 5 Ma (Fig. 6). These dates are similar to those reported for *Cyrtandra* in Roalson and Roberts (2016) and Johnson et al. (2017) and significantly younger than those reported in Clark et al. (2008, 2009). These last, much earlier, dates were based strictly on the geological ages of islands, an approach which has been shown to be problematic (Renner 2005, Heads 2011). The slightly younger stem age recovered in the present analysis is likely due to the inclusion of *Loxostigma,* an outgroup taxon that is more closely related to *Cyrtandra* than those used in earlier *Cyrtandra*-focused studies.

This pattern of origin in the mid Miocene and young species, mostly the result of speciation in the last 5 My, is reported in other Southeast Asian taxa such as *Begonia* (Thomas et al. 2012) and *Aglaia* (Grudinski et al. 2014), and it is highlighted by de Bruyn et al. (2014) in their meta- analysis of regional biodiversity. There are a number of geological factors which are likely to have been drivers of diversification during this period. Approximately 23 Ma the Sunda and Sahul shelves moved closer together, creating land in the centre of the region for the first time (Hall 2002, 2012a, b). The subsequent rapid orogenesis on key islands such as Sulawesi and New Guinea (Hall 2002, Hall 2012a, b) also created new habitat. Finally, the climate and sea- level fluctuations of the Pleistocene resulted in cyclic vicariance with frequent habitat fragmentations and amalgamations (Voris 2000, Woodruff 2010, Cannon 2012, Morley 2012).

The mean diversification rate for *Cyrtandra* in Southeast Asia is 0.49 net speciation events per million years, significantly higher than the rate of 0.089 calculated by Magallon and Sanderson (2001) for angiosperms as a whole. The rates of Southeast Asian *Cyrtandra* diversification are comparable to that of the ecologically similar mega- diverse genus *Begonia* in the Neotropics (0.5) and in Asia (0.61) (Moonlight et al. 2015). They are slightly slower than in Pacific *Cyrtandra,* which has a rate of 0.68 (Roalson and Roberts 2016), and significantly slower than lineages of Hawaiian *Cyrtandra,* in which diversification rates as high as 3.5 are reported (Johnson et al. 2019). In the case of the Pacific radiation, Roalson and Roberts (2016) suggested that geography may have played a significant role in the rapid diversification of taxa, with the emergence of many island archipelagos in the last 5 Ma. Additionally, a transition to fleshy fruits may have aided long- distance dispersal by avian frugivores from source areas in Southeast Asia, followed by diversification in newly colonised island regions.

Ancestral range estimation

The island of Borneo emerges as the most likely ancestral area for the genus and for many of the early diverging clades of *Cyrtandra* (Fig. 7). Burtt (2001) speculated that Borneo represented the 'original heartland' of the genus based on its high species numbers (c. 200) and the abundant morphological diversity seen here, including richly developed anatomical characters such as sclereids and tracheoids, which 'decrease in all directions' from this centre. The combination of Borneo's large area, relatively stable geological history (Hall 2012, De Bruyn et al. 2014), and extensive areas of rainforest, even during glacial maxima (Cannon 2012), offer a compelling explanation for this lineage accumulation and *in-situ* diversification. The majority of samples from Borneo in this analysis are from NE Borneo. Increased sampling from elsewhere on the island, particularly the under- collected areas of Kalimantan, will help clarify whether Borneo's important role in the development of biogeographic patterns in the region, is largely due to the key role of NE Borneo's three highest mountains as significant rainforest refugia (as reported for birds; Sheldon 2016) or whether it is more generally attributable to the island as a whole.

With an estimated ancestral range on the Sunda Shelf, *Cyrtandra* is another example of the increasingly well- documented movement of taxa from the west to east of Southeast Asia, particularly in rainforest lineages (Su and Saunders 2009, Richardson et al. 2012, Thomas et al. 2012, Grudinski et al. 2014, Crayn et al.

2015). There are examples of dispersal in the opposite direction, such as in Proteaceae (Barker et al. 2007) and Myrtaceae (Sytsma et al. 2004), but there is a distinct asymmetry (Richardson et al. 2012, Crayn et al. 2015). The west-to-east dispersal appears to have been particularly prevalent from the mid-Miocene onwards as warmer and wetter conditions prevailed, rainforest expanded and extant land emerged east of Wallace's Line (Richardson et al. 2012, Grudinski et al. 2014, Crayn et al. 2015).

The earliest example of a Sahul–Sunda long distance dispersal in this study is within Clade E at 9.6 Ma (7.64-11.68 Ma, 95% HPD) from Sunda to Sahul. This comfortably within the time-frame of Sahul-Sunda disjunction events compiled by Crayn et al. (2015). Many of the *Cyrtandra* taxa east of Wallace's Line are characterised by fleshy berries as opposed to the predominantly dry indehiscent capsules of the Sunda shelf taxa (Fig. 1; Burtt 2001, Johnson et al. 2017). This change in fruit morphology is possibly associated with a transition in dispersal mode from small mammal dispersal to bird dispersal (Gillett 1967, Burtt 2001). A zoochorous dispersal mode is presented by Crayn et al. (2015) as being the most prevalent for Sunda–Sahul dispersals, with 90% of ancestral species possessing zoochorous propagules, and it seems likely that the transition to fleshier berries has facilitated dispersal of *Cyrtandra* across the region. As the majority of the species in the Sahul clade (Clade E), including *C. vittata* and *C. bungahijau* from New Guinea, *C. baileyi* from Australia, and *C. subulibractea* from the Solomon Islands, have fleshy fruits (Gillett 1975, Atkins et al. 2019), it seems likely that it is the ancestral state for this clade.

Biogeographic patterns

Borneo and the islands of the Sunda shelf

Borneo is the source of the highest number of dispersal events for Malesian *Cyrtandra*, with dispersals to the Philippines, Sulawesi, Sumatra, Peninsular Malaysia, Java, and New Guinea originating here (Fig. 8). This is consistent with De Bruyn et al.'s (2014) characterisation of the island as an evolutionary hotspot defined not only in terms of high species numbers and *in situ* diversification but also subsequent emigration. High dispersal levels between the islands on the Sunda shelf reflect the shared geological history of these continental islands, which would have formed continuous land during at least some of the glacial maxima (Voris 2000, Hall 2012). At these times there would also have been more extensive areas of rainforest (Cannon et al. 2009, 2014, Cannon 2012), facilitating exchange and dispersal in a wet forest genus like *Cyrtandra.* There are only two samples from the Sunda shelf that fall within the large, predominantly Wallacean, clade (Clade J, Fig 5), and these are both from Central Java, confirming Java's position as anomalous, with links both to the Sunda shelf and Wallacea, as reported by Van Welzen et al. (2011) in their phytogeographic study of the region.

Philippines

The Philippines represent an important secondary source area for *Cyrtandra,* as well as a stepping-stone for dispersal to some of the more distant regions such as Taiwan and Japan and New Guinea (Fig. 8, Table 6). Dispersal events from the Philippines were recovered south to Sulawesi, north to Taiwan and southern Japan, east to New Guinea, and even south-west to Java. The very different position of the Philippine islands 10 Ma, when *Cyrtandra* was diversifying, with southern Philippine islands such as Mindanao located much closer to the equator (Hall 2002, Hughes et al. 2015), offers an explanation for the key role of the Philippines as a route through the region. The Philippines is an area of high species diversity for the genus, with c. 150 species already recorded and new species still being described (Olivar et al. in press). Species from these islands are morphologically very diverse and there are a number of species with fleshy fruits in the Philippines, notably *C. hirtigera* from Palawan and *C. fragilis* from Negros and Mindanao, which is congruent with the high vagility of lineages in the Philippine clades. For *Cyrtandra*, the earliest diverging branch of Philippine taxa are from Palawan and Camiguin (Clade G), dating to just before 10 Ma, suggesting that the Philippines were colonised relatively early in the diversification of the genus and that both short and longer distance dispersal from Borneo played a part in the colonisation of the archipelago. Our results provide some support for the theory that Palawan, or some part of it, could have been above sea level significantly earlier than the start of the Pliocene c. 5 Ma, as proposed for the Palawan Ark Hypothesis (Blackburn et al. 2010, Siler et al. 2012). These results would also require Camiguin to be above sea level earlier than the estimated 2 Ma maximum age for this island (Steppan et al. 2003), although incomplete sampling, particularly from nearby islands in the archipelago, could also explain the discrepancies in dates.

Sulawesi

Sulawesi is an area of significant immigration, being the recipient of 20% of all dispersals, the joint highest in our analysis (Table 6), with dispersals from Java, the Philippines and Borneo. In contrast, dispersal events from Sulawesi to surrounding islands were very infrequent (0.5 events to Sumatra and 0.2 events to the Philippines, Table 6, Fig. 8). It is notable that although fleshy fruited *Cyrtandra* species, such as the unusual epiphytic *C. purpurea,* occur on Sulawesi, the majority of species, and all of the most common species, on the island, such as *C. hypogaea, C. polyneura* and *C. kinhoii,* are characterised by the drier, tough-walled fruits typical of the Sunda shelf. This low level of emigration and the relative insignificance of Sulawesi in terms of a dispersal route across the region is, however, also seen in other groups such as *Begonia* (Thomas et al. 2012). Sulawesi is encircled by biogeographic boundaries, including Wallace's and Huxley's line to the west, and Weber's and Lydekker's to the east, suggesting that there are real barriers to dispersal in this area. However, immigration on to the

island, particularly from the Philippines and Borneo across the western lines, has clearly occurred more than once in *Cyrtandra*. Sulawesi's highly dynamic geological history (Hall et al. 2012a, Stelbrink et al. 2012) and the resultant increase in habitat diversity and available niche space for colonising species, offers a possible explanation for the high level of immigration and establishment on the island. Dispersal back across Wallace's line from Sulawesi and successful establishment on the Sunda shelf islands appears to have been difficult for *Cyrtandra,* possibly due to niche pre- emption in the older, more established forests of those islands. Increased sampling of *Cyrtandra* from the islands east of Sulawesi, particularly from the Moluccas and New Guinea, will help illuminate whether there is a barrier in this direction or whether this is an artefact of sampling.

New Guinea and the Pacific

New Guinea is resolved as the most likely source of dispersals to Australia, the Solomon Islands, and French Polynesia for *Cyrtandra* (Fig. 8, Table 6). West- to- east dispersal patterns have been well documented from New Guinea into the eastern Pacific (Keast 1996). *Cyrtandra* is notable for being the only Malesian Gesneriaceae genus with a distribution that extends significantly into the Pacific (Hilliard and Burtt 2002). The large Malesian genera *Aeschynanthus* and *Agalmyla* have wind- dispersed seeds and, despite being highly diverse in New Guinea, do not extend beyond the Solomon Islands and the Louisade Archipelago (Hilliard and Burtt 2002), respectively. Johnson et al. (2017) reported strong asymmetry in the direction of founder events in their study of *Cyrtandra* in the Pacific, with the majority of dispersals occurring from a west- to- east direction, which they postulated to be the result of bird dispersal. The routes to Australia and the Solomon Islands found here were reported by Johnson et al. (2017) and were suggested by Gillett (1975) based on his extensive knowledge of the *Cyrtandra* of New Guinea and the Pacific. He reported strong morphological affinities between the *Cyrtandra* of New Guinea and the Bismarck Archipelago and Solomon Islands, and an attenuation of morphological diversity with increasing distance from New Guinea into the Pacific (Gillett 1975). The longest- distance dispersal event in this study is from New Guinea (Clade I, from Mt Jaya in the far western part of the main cordillera) to the Marquesas/Society Islands. However, this result is most likely an artefact of the relatively low level of sampling from the South Pacific in this study. In the study by Johnson et al. (2017), which included higher density sampling of Pacific taxa, the Marquesan lineage is the result of a single dispersal event from Samoa, while the Society Islands taxa are the result of two dispersal events, one from Fiji and one from Samoa.

Conclusions

Using a robust and well sampled phylogenetic tree to study evolutionary relationships and biogeographical processes in Southeast Asian *Cyrtandra*, we found evidence in support of (i) Borneo as the most likely ancestral area for the genus, (ii) west- to- east dispersal across the region and into the Pacific, (iii) the Philippines as an important secondary source area and stepping stone to Wallacea, Taiwan and Japan, and New Guinea, and (iv) a mid- Miocene origin for the genus with most of the extant diversity being the result of speciation in the last 5 Ma. These patterns are increasingly well- documented and are beginning to form an emerging paradigm for Southeast Asian plant biogeography. The present study has provided further insight into the fundamental questions of when and where plant diversification took place in Southeast Asia and the role of geo- tectonic and climatic processes in shaping the floristic composition of the area and setting the stage for significant species diversifications. Further work is needed to understand niche evolution and the genomic basis of adaptation to unravel how the massive species richness of *Cyrtandra* evolved and how it is maintained.

Acknowledgements

We thank the Edinburgh Botanic Garden (Sibbald) Trust, the Elvin McDonald Research Endowment Fund (The Gesneriad Society), the RBGE Travel Fund, the James & Eve Bennett Trust, the Royal Horticultural Society, and Davis Expedition Fund for funding. The Royal Botanic Garden Edinburgh is supported by the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government.

In Indonesia, we would like to thank RISTEKDIKTI, the Indonesian Ministry of Forestry, and staff at the Kebun Raya Bogor, Herbarium Bogoriense, Forestry Research Institute of Manado and Andalas University. We particularly thank Joeni Rahajoe, Wisnu Ardi, Marlina Ardiyani, Hendrian, Julianus Kinho, Deden Girmansyah, and Nurainas for assistance with permits and collecting. In Malaysia, we would like to thank staff at the Forest Research Institute Malaysia, particularly Ruth Kiew and Sam Yen Yen, the Tree Flora of Sabah and Sarawak programme, Postar Miun, Joan Pereira, Susana Sabran, and Julia Sang. Fieldwork in the Philippines over many years was facilitated by the Philippine National Herbarium, Mina L. Labugen (DENR), and Aurea L. Feliciana (Isabela State University). We would also like to thank Masatsugu Yokota (Univ. Ruykyus, Japan) and Ching- I Peng (Academia Sinica, Taiwan).

Additional samples were generously provided by RBG Kew, Shelley James (Florida Museum of Natural History, Bishop Museum, Honolulu), Wisnu Ardi (Bogor Botanic Garden), Deden Girmansyah (Herbarium Bogoriense), M. Poopath (Thailand), and Michael Kiehn (Vienna Botanic Garden); and from RBGE (in alphabetical order) George Argent, Sadie Barber, B.L.Burtt, Quentin Cronk, Andy Ensoll, Louise Galloway, Olive Hilliard, Mary Mendum, David Middleton, Mark Newman, Axel Poulsen, Carmen Puglisi, Steve Scott, Daniel Thomas, and Peter Wilkie.

We would like to thank Prof Gao Lian Ming, Kunming Institute of Botany, Chinese Academy of Sciences,

Yunnan, China, for the gift of cpDNA sequences of two of the outgroup samples which was funded by Grant No. 2017- LSFGBOWS- 01 from the Large- scale Scientific Facilities of the Chinese Academy of Sciences.

At RBGE, we would like to thank Steve Scott, Sadie Barber, and Nathan Kelso for excellent care of the *Cyrtandra* living collections, and Michelle Hart, Laura Forrest, and Ruth Hollands for expert advice in the molecular laboratories. Assistance with the programme BioGeoBEARS was generously given by Nick Matzke. Thanks also to Jay Edneil Olivar for enormous help with naming of the Philippine samples included in the analysis.

Supplementary Materials

The following materials are available as part of the online article from https://escholarship.org/uc/fb

Table S1. Taxon list for samples in the current study.

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Submitted: 20 July 2019
First decision: 30 August 2019
Accepted: 24 December 2019

Edited by Roy Erkens and Robert J. Whittaker

Appendix 3: Atkins, H.J., Heatubun, C.D., Galloway, L. & Bramley, G.L.C. 2019. Two new species, *Cyrtandra bungahijau* and *C. vittata,* and notes on *Cyrtandra* (Gesneriaceae) from Yapen Island, Indonesia. *Kew Bulletin* 74: 29 https://doi.org/10.1007/s12225-019-9817-2

KEW BULLETIN (2019) 74: 29
DOI 10.1007/S12225-019-9817-2

ISSN: 0075-5974 (print)
ISSN: 1874-933X (electronic)

Two new species, *Cyrtandra bungahijau* and *C. vittata*, and notes on *Cyrtandra* (Gesneriaceae) from Yapen Island, Indonesia

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Summary. Two new species of *Cyrtandra* (Gesneriaceae) are described; one apparently endemic to Yapen Island, Tanah Papua, the other present in Tanah Papua and in Papua New Guinea: both species are described and illustrated, and preliminary conservation assessments given. Notes on the identity of other known collections of *Cyrtandra* from Yapen are provided.

Key Words. New Guinea, Papua New Guinea.

Introduction

Cyrtandra J.R.Forst. & G.Forst. is a large genus of c. 800 species of herbs, shrubs, climbers, and small trees (Atkins *et al.* 2013). It is a predominantly Southeast Asian genus and is found from the Nicobar Islands in the Indian Ocean, throughout Malesia, in Taiwan and the southern Japanese islands, in northern Australia and east across Polynesia to Hawaii. It is recorded on the Asian continent only as far north as central Thailand. Its centres of diversity are New Guinea and Borneo (each with over 100 species) and the Philippines (with over 80 species) (Atkins *et al.* 2013). It is found in the rainforest, from sea level to over 3000 m.

The New Guinean island of Yapen in the Indonesian province of Papua is located in Cenderawasih Bay. The island has been selected as an area for priority conservation by Conservation International (Supriatna 1999), a World Wildlife Fund ecoregion (WWF n.d.), and designated as a natural reserve by the Indonesian Ministry of Forestry in 1982 for its unique bird life (Beehler 2007) and limestone and ultramafic flora (Johns 1997). Although several endemic species have been recorded (Johns 1995; Hughes *et al.* 2015), there has been relatively little botanical exploration on Yapen (Conn 1994; Johns 1997; Frodin 2007; van Steenis Kruseman n.d.), and certainly no prior focus on *Cyrtandra*. In 1923, Schlechter published his '*Gesneriaceae Papuanae*', which included a revision of *Cyrtandra* across the whole of New Guinea with 54 newly described species (Schlechter 1923). Prior to this, new species had been published in various accounts resulting from major expeditions to New Guinea (Schumann & Lauterbach 1901; Lauterbach 1910; Moore 1916). Clarke's monograph of *Cyrtandra* (Clarke 1883) across its distribution, only recognised five species and one variety from New Guinea. Schlechter (1923) divided 87 of the 96 *Cyrtandra* species he recognised into two subgenera and 14 sections, leaving nine unplaced, four of which were only noted as being new and not formally described. The subgenera were distinguished by corolla morphology; sections generally by combinations of characters. Species published from New Guinea since Schlechter (1923) have been from mountainous areas on the mainland (Burtt 1971; van Royen 1983).

To date, no *Cyrtandra* species have been specifically described from Yapen, and the island has not been listed in any species' distribution notes. We have only been able to source specimens that were collected in 1939 on an expedition by van Dijk, a Dutch Forest Officer, to Yapen (Jappen) and Biak islands (van Steenis Kruseman, n.d.). Frodin's detailed account of biological exploration of New Guinea in the '*Ecology of Papua*' series (Frodin 2007), does list a number of earlier expeditions that went to Yapen, but many of these seem to have had a non-angiosperm focus (e.g. Crown Prince Leopold of Belgium, 1929 [only algae, lichen and mosses]; E.L.Cheeseman, 1938 – 39 [mainly entomology]), and after searching the collections at BM, E, K and L, we haven't found any further specimens (herbarium acronyms follow Thiers [continuously updated]).

Accepted for publication 22 May 2019. Published online 3 July 2019

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Joint fieldwork between staff of the Royal Botanic Garden Edinburgh and Universitas Papua in 2009 resulted in the acquisition of two living collections of *Cyrtandra*. It has not been possible to match these plants with any known species or any of the Yapen *Cyrtandra* specimens that we have located. Here we present a description and illustration of the two new species, *C. bungahijau* Bramley & H.J.Atkins and *C. vittata* Bramley & H.J.Atkins, as well as notes on the other Yapen collections known to us.

Materials and Methods

All available type specimens of New Guinea *Cyrtandra* (held at B (online), BM, E, K, L (online), P (online)) were examined to establish the identity or novelty of the collections from Yapen Island. The descriptions were based on living material in cultivation at the Royal Botanic Garden Edinburgh (RBGE), photographs of plants growing in the field, and herbarium and spirit material. All cited specimens have been seen by the authors.

The proposal for IUCN conservation categories was made following the IUCN Red List Categories and Criteria and associated guidelines (IUCN 2012).

Taxonomic Treatment

Cyrtandra bungahijau *Bramley & H.J.Atkins* sp. nov. Type: Indonesia, Tanah Papua, Yapen Island, Kosiwo, Ambaidiru, Kapit Atusamban behind the homestay in Ambaidiru Village, 1000 m, cuttings collected 18 Feb. 2009, *Argent et al.* ABEG 218, cultivated at RBGE as 20090826, vouchered as *Atkins* 57 (holotype E!; isotype MAN!).

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Stocky shrub to 75 cm. *Stems* thick, tessellate, corky, glabrous. *Leaves* opposite; those of a pair subequal or with one significantly larger than the other but both well developed; petioles c. 5 mm, somewhat corky, tessellate, glabrous; blades 7 – 15 (– 30) × 4 – 7 (– 15) cm, elliptic, thick, leathery, apex short acuminate, acumen 2 – 3 mm, base decurrent, margin distantly serrulate to almost entire; 7 – 8 pairs of lateral veins, tertiary venation reticulate, sparse and feint on upper surface, obscure below, upper surface of mature leaves mid green with a covering of coarse white hairs, lower surface light green, sparsely hairy, more densely so on midrib and veins. *Inflorescence* subsessile, axillary, 1 – 2-flowered. *Bracts* green, triangular, c. 7.5 × 5 mm, glabrous internally, externally with a fringe of coarse white hairs along the midvein and apically. *Calyx* green, tubular, c. 13 mm long, five-lobed but appearing three-lobed at apex, lobes c. 4 mm long, acute at apex, with coarse, white hairs externally. *Corolla* light green, narrow tubular, 25 mm long, glabrous towards base whilst inside calyx, becoming densely white hairy externally in the upper half, lobes extending forward, not spreading or recurved, mouth of corolla barely open, lobes oblong, somewhat acute at apex, upper lobes c. 3 × 2 mm, lower lobes c. 2 × 3 mm, internally with a dense covering of glandular hairs in upper half of tube and on the lower lobes and with two very small outgrowths at the point of insertion of the filaments. *Filaments* white, straight, glabrous, c. 5 mm long, borne c. 15 mm from base of corolla. *Anthers* white, c. 2 mm long, thecae slightly divaricate, glabrous, with a short connective at the tips. *Lateral staminodes* c. 1 mm long, *central staminode* c. 0.5 mm. *Gynoecium* c. 22 mm long overall; disk cupular with undulate margin, slightly lower on one side, c. 1.5 mm, glabrous; ovary glabrous; style sparsely glandular hairy; stigma bilobed, lobes c. 1.5 mm long, pressed together on specimens seen. *Fruit* not seen. Figs 1 & 2.

RECOGNITION. *Cyrtandra bungahijau* Bramley & H.J.Atkins is most similar to *C. jadunae* Schltr., in section *Pachycyrtandra* Schltr., but can be distinguished from it by its leaf bases (decurrent vs cuneate), calyx lobes (4 mm vs 12 mm) and internal corolla indumentum (glandular hairy vs glabrous).

DISTRIBUTION. Indonesia: Papua, Yapen Island. See Map 1.

SPECIMENS EXAMINED. INDONESIA. Tanah Papua, Yapen Island, Kosiwo, Ambaidiru, Kapit Atusamban behind the homestay in Ambaidiru Village, 1000 m, cuttings collected 18 Feb. 2009, *Argent et al.* ABEG 218, cultivated as 20090826, vouchered as *Atkins* 57 (E, MAN).

HABITAT. Disturbed secondary forest; alt. 1000 m.

CONSERVATION STATUS. Due to the lack of collecting activity on Yapen or detailed information about threat, a conservation category of Data Deficient (DD) is proposed for this species and we emphasise the need for further survey work in this area.

ETYMOLOGY. This species is named for its distinctive green corolla; bunga hijau means 'green flowers' in Bahasa Indonesia.

NOTES. This species falls within Schlechter's subgenus *Cyrtandra*, section *Pachycyrtandra*. The subgenus contains those species that do not have strongly zygomorphic corollas and the section contains species with single or paired, large, densely hairy flowers and subequal well-developed leaves. The fruit of this new

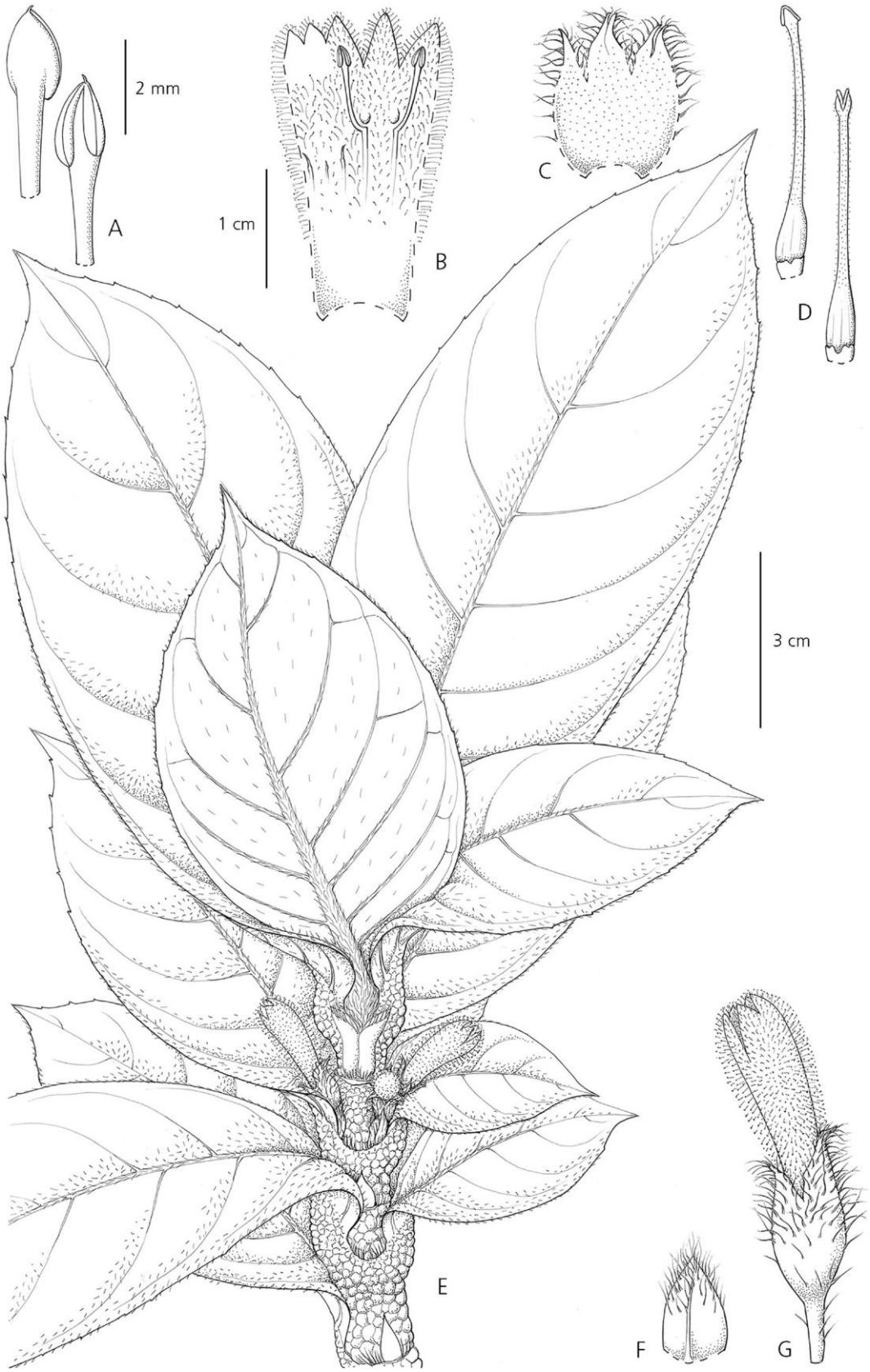

Fig. 1. *Cyrtandra bungahijau*. A anthers; B corolla, longitudinal section; C calyx, longitudinal section; D gynoecium; E habit; F bract; G flower, lateral view. From *Atkins* 57 (E). DRAWN BY CLAIRE BANKS.

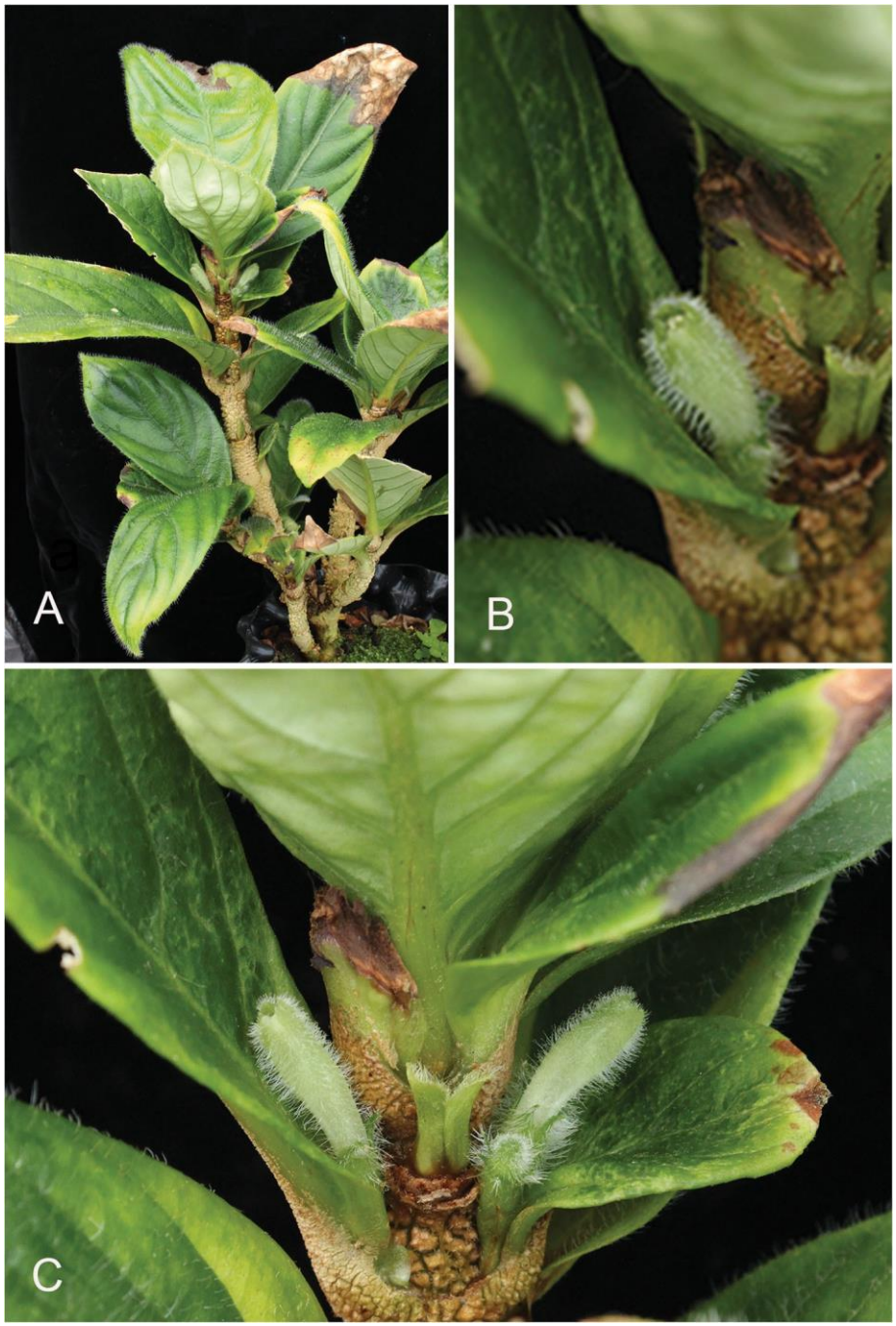

Fig. 2. *Cyrtandra bungahijau*. A habit; B & C flowers in leaf axils. (RBGE20090826 vouchered as *Atkins* 57) PHOTOS: SADIE BARBER.

species has not been seen but others in this section have persistent calyces in fruit. Within the section, this new species is most similar to *C. jadunae* Schltr. from 'Jaduna' on the Waria River in Morobe Province, Papua New Guinea. Although the type of *C. jadunae* (*Schlechter* 19331) has not been found, comparison with Schlechter's description shows that the two species share glabrous ovaries and stamens that do not exceed the corolla but differ in the leaf bases (decurrent vs cuneate), the more deeply divided calyx in *C. jadunae*, and variation in indumentum inside the corolla (glabrous in *C. jadunae* and glandular hairy in *C. bungahijau*).

Cyrtandra vittata *Bramley & H.J.Atkins* sp. nov. Type: Papua New Guinea, Huon Peninsula, Cromwell Mts, 22 Oct. 2006, *de Kok* 1156 (holotype K!, isotype LAE!).

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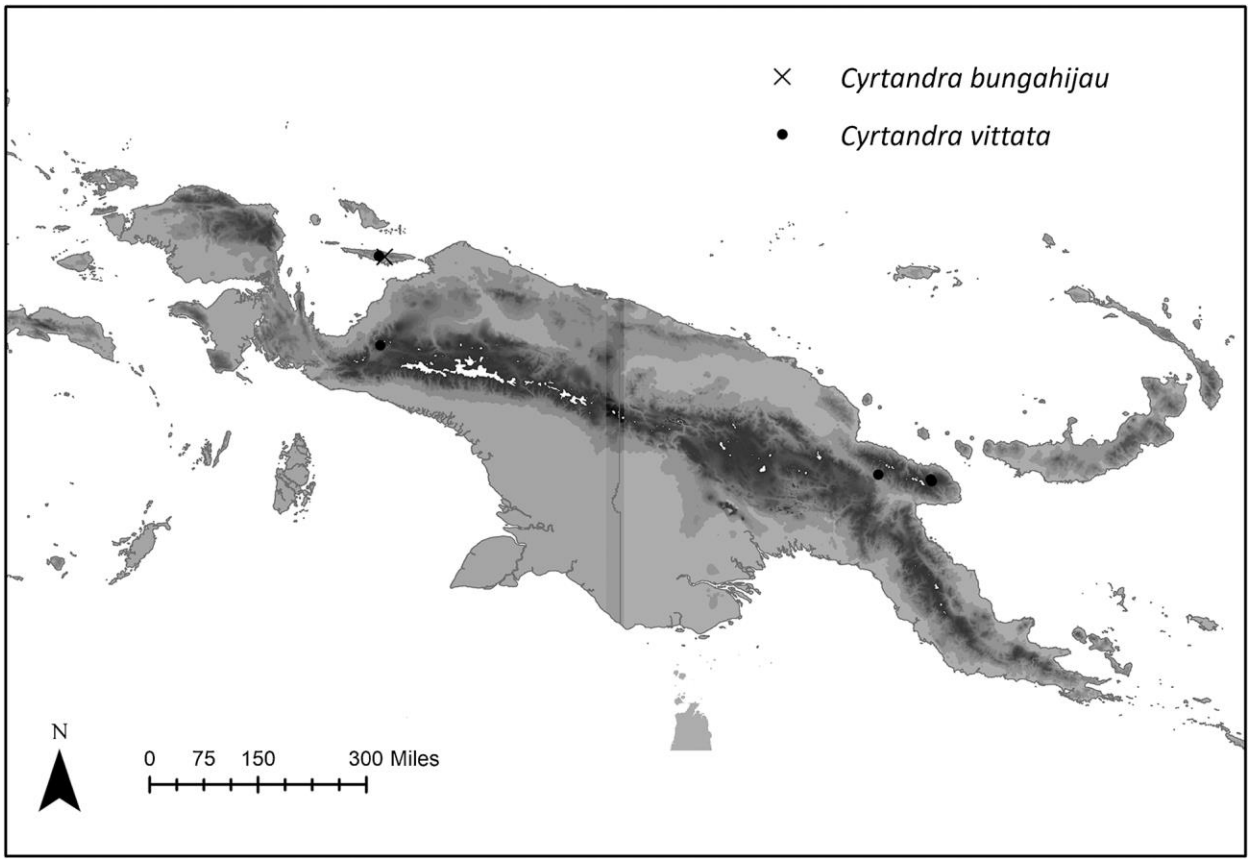

Map 1. Known distribution of *Cyrtandra bungahijau* and *C. vittata*.

Sparingly branched shrub to 1 m. *Stems* woody at base, striate, glabrate, sparsely hairy on young growth. *Leaves* opposite, those of a pair subequal to strongly anisophyllous; petioles of major leaf 9 – 20 mm, hairy elliptic to slightly obovate; blades of subequal leaves and major leaf in anisophyllous pairs (7 –) 9 – 15 (– 21) × (2 –) 3.5 – 5.5 (– 6.4) cm, apex long acuminate, up to 20 mm, base cuneate, not decurrent, slightly asymmetrical, margin distantly serrate, the serrations often irregular; 5 – 8 (– 10) pairs of lateral veins, tertiary venation reticulate, sparse, upper surface of leaves mid green, slightly mottled, sparsely hairy, lower surface light green, sparsely hairy, more densely so on midrib and veins; petiole of minor leaf c. 5 mm or leaf sessile; blades elliptic, 1.8 × 0.5 cm to stipule-like, 0.55 – 1 cm long. *Inflorescence* sessile, in leaf axils or where leaves have fallen, 1– 6-flowered, fasciculate. *Bracts* linear, c. 2 mm long, hairy, light green, tinged red. *Pedicel* light green, tinged red, 9 – 10 mm, hairy. *Calyx* dull red, tinged slightly green at apex and along central rib of each lobe, (8 –) 10 – 12 mm long, hairy externally, evenly 5-lobed or upper three lobes slightly closer together than to the lower two, lobes 5 – 7 mm, narrow acuminate. *Corolla* cerise pink with white longitudinal stripes running along the length of the corolla from the tip of the lobes to the base, funnel-shaped, arcuate, held upright, somewhat laterally flattened, 27 – 30 mm long, with a covering of short, white eglandular hairs externally, lobes recurved, triangular, upper lobes 1.5 – 2 × c. 3 mm, lateral lobes 6 – 8 × c. 4 mm and lower lobe 5 – 7 × c. 5 mm, inside of lobes densely glandular hairy. *Filaments* white, straight, 15 – 18 mm long, borne c. 10 mm from base of corolla, sparsely glandular hairy towards the apex. *Anthers* white, c. 2 mm long, cohering at tips before dehiscence, thecae parallel. *Lateral staminodes* c. 6 mm, *central staminode* c. 2 mm. *Gynoecium* 22 – 30 mm long overall; disk cupular but much lower on one side, with undulate margin, glabrous, c. 2 mm; ovary more or less glabrous or with some tiny hairs and a few scattered glands; style densely glandular hairy particularly towards apex; stigma bilobed, flattening out when mature and appearing almost peltate, c. 1 mm across, white. *Fruit* green when young, turning white with age, cylindrical, c. 20 × 4 mm when dried,

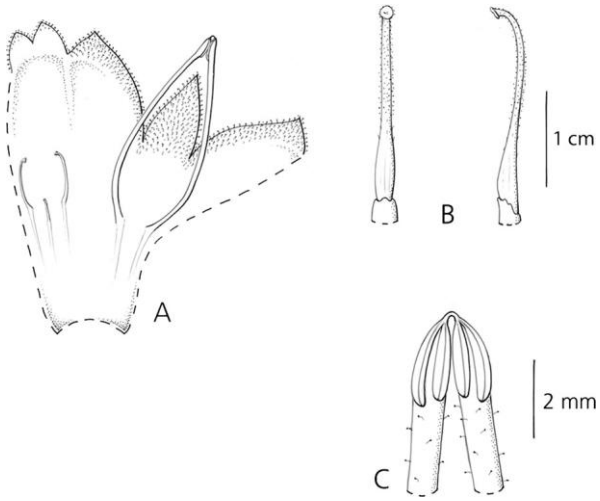

Fig. 3. *Cyrtandra vittata*. A corolla, longitudinal section; B gynoecium; C anthers. From *Atkins* 14 (E). DRAWN BY CLAIRE BANKS.

smooth and glabrous, calyx and base of style not persistent. *Seeds* small, numerous. Figs 3 & 4.

RECOGNITION. *Cyrtandra vittata* Bramley & H.J.Atkins is most similar to *C. minjemensis* Schltr., in section *Loxanthe* Schltr., but can be distinguished by its striped pink and white corolla (vs purple corolla) and caducous calyx (vs persistent calyx).

DISTRIBUTION. Indonesia: Papua; Papua New Guinea: Morobe. See Map 1.

SPECIMENS EXAMINED. PAPUA NEW GUINEA. Morobe: Huon Peninsula, Cromwell Mts, 22 Oct. 2006, *de Kok* 1156 (K, LAE); Indagen, 30 Oct. 2006, *de Kok* 1263 (E, K, LAE); Umi R., Markham Valley, 26 Nov. 1959, *Brass* 32708 (E, K). INDONESIA. Tanah Papua: Wissel Lake Region [Paniai Lakes], Djembodini-Kerimamba, 27 Feb. 1939, *Eyma* 4634 (K, L); Yapen Island, Kosiwo, Ambaidiru, Kapit Atusamban, 893 m, 19 Feb. 2009, *Argent et al.* ABEG 227, cultivated at RBGE as 20090734, vouchered as *Atkins* 14 (E, MAN).

HABITAT. Primary forest, often with some degree of disturbance; alt. 480 – 2000 m

CONSERVATION STATUS. The unusual distribution pattern of this species gives a preliminary conservation assessment, using GEOCAT (Bachman *et al.* 2011), of LC (Least Concern) based on EOO, and EN (Endangered) based on AOO using a cell width of 2 km. We suggest that, given the lack of collecting activity across the centre of this distribution (Gideon 2015), and the consequent likely underestimation of extent, that this species is listed as Least Concern.

ETYMOLOGY. This species is named for the distinctive vertical stripes on the corolla.

NOTES. This species falls within Schlechter's subgenus *Glossophorae* due to its strongly zygomorphic corolla. Within the subgenus, it can be tentatively placed in his section *Loxanthe* due to its mostly anisophyllous leaf arrangement, short brown indumentum, glabrous ovary, lack of outgrowth in the corolla tube and deeply divided calyx lobes. Species within this section should, however, also retain their calyx in fruit. We have only seen fruit on the cultivated plant, and in this case, the calyx is clearly caducous.

Within this section, *Cyrtandra vittata* most closely resembles *C. minjemensis*. We located two isotypes of this species (BO, P) but, unfortunately, both were sterile. We obtained permission from the Curator responsible for destructive sampling at P, Dr Myriam Gaudeul, for material from the type for DNA extraction to confirm if the type of *C. minjemensis* was definitely distinct from the new material but we were, unfortunately, not successful in obtaining DNA. Despite an absence of molecular confirmation, sufficient differences with the original description of *C. minjemensis* including corolla colour (purple vs pink and white striped) and calyx persistence in fruit persuaded us that this should best be described as a distinct taxon.

The distribution of *Cyrtandra vittata* (see Map 1) is unusual both in its extent and also the marked disjunction between Tanah Papua and Morobe. From our initial taxonomic work, it appears that the distributions of some *Cyrtandra* species in New Guinea are wider than we have found to be typical in other areas of Malesia. From the literature, and discussions with colleagues, we have found examples of species that are distributed along the northern coast of New Guinea, some continuously, such as *Medusanthera laxiflora* (Miers) R.A.Howard (Utteridge 2011), and others patchily such as *Actinodaphne multiflora* Benth. and *Schefflera waterhousiae* Harms. (both D. Frodin, pers. comm.). These species are all likely to be dispersed by frugivorous birds: the patchy distributions could be due to lack of botanical collections across the area (Gideon 2015), or to the route of the dispersers. Perhaps the apparent distribution of *C. vittata* is a reflection of lower collecting density in western Papua New Guinea and eastern Tanah Papua, and further fieldwork would result in more records of it being found. As for the dispersal of *C. vittata*, we have no observations, but could speculate that the fleshy white fruit is dispersed by columbiform birds, as has been suggested for dispersal of *Cyrtandra* species across the Pacific to the Hawaiian archipelago (Cronk *et al.* 2005).

Fig. 4. *Cyrtandra vittata*. A inflorescence; B mature fruits; C immature fruit; D habit; E inflorescences; F flower, lateral view. A – D (RBGE20090734 vouchered as *Atkins* 14); E – F *de Kok* 1156. PHOTOS: A, D LYNSEY WILSON; B, C HANNAH ATKINS; E, F ROGIER DE KOK.

The collections from both extremes of this distribution are morphologically very similar and *Atkins* 14, from Yapen, and *de Kok* 1156 and *de Kok* 1263 from Morobe resolve as sister in an as yet unpublished phylogeny of *Cyrtandra.*

Two additional collections, *Takeuchi* 8618, also from Morobe, and *Takeuchi* 11289, from Chimbu Province in the Highlands Region, are similar in having pink/red and white striped corollas and are possibly closely related but have larger, more leathery leaves and larger flowers. The corolla is significantly longer, up to 40 mm long, with filaments that far exceed the mouth of the corolla at maturity, and the nectary disk is not distinctively lower on one side.

Notes on other Yapen collections

One of the authors (GLCB) is in the process of revising Papuan Cyrtandras. The notes that follow represent our preliminary attempts to identify the other collections known to us from Yapen, and to assign them to the sections described by Schlechter (1923). Until more detailed taxonomic research is completed, using Schlechter's work is the most practical method of specimen identification. We aim to establish whether Schlechter's sections represent monophyletic groups through future phylogenetic studies.

1. Cyrtandra decurrens var. puncticulata *C.B.Clarke*

Not assigned to section

SPECIMENS EXAMINED: Indonesia, Papua, Pulau Yapen: *Aet & Idjan* 153 (L).

2. Cyrtandra janowskyi *Schltr*.

Subgen. *Cyrtandra*; sect. *Leucocyrtandra* Schltr.

SPECIMENS EXAMINED: Indonesia, Papua, Pulau Yapen: *Aet & Idjan* 698 (L).

3. Cyrtandra suberosa *Schltr.*

Subgen. *Glossophorae*; sect. *Centrosiphon* Schltr.

SPECIMENS EXAMINED: Indonesia, Papua, Pulau Yapen: *Aet & Idjan* 201 (K, L).

4. Cyrtandra sp. *indet*.

Subgen. *Cyrtandra*; sect. *Axillanthe* Schltr.

SPECIMENS EXAMINED: Indonesia, Papua, Pulau Yapen: *Aet & Idjan* 82; 232 (both at L).

5. Cyrtandra sp. *indet*.

Not assigned to section

SPECIMENS EXAMINED: Indonesia, Papua, Pulau Yapen: *Aet & Idjan* 460 (L).

6. Cyrtandra sp. *indet.*

Not assigned to section

SPECIMENS EXAMINED: Indonesia, Papua, Pulau Yapen: *Argent et al.* ABEG 205 (E).

Acknowledgements

We thank the curators of the herbaria cited above for access to or loan of material, and Dr Myriam Gaudeul (P) for providing material for DNA extraction from the isotype of *Cyrtandra minjemensis*; Claire Banks for the detailed illustrations; Sadie Barber, Lynsey Wilson and Rogier de Kok for permission to use their photographs, and Nathan Kelso and Sadie Barber for excellent care of the living collections. GLCB is grateful to Tim Utteridge and David Frodin for informative discussions on species distributions in northern New Guinea. The new taxon was collected on Yapen Island during the Papua expedition of the Royal Botanic Garden Edinburgh in 2009, in which LG and CDH were involved. LG and CDH would like to thank Kementerian Riset dan Teknologi Republik Indonesia, Lembaga Ilmu Pengetahuan Indonesia, Universitas Papua, Kebun Raya Cibodas, Balai Penelitian Kehutanan Manokwari, BKSDA Papua I Sub Seksi Pulau Yapen, authorities in Serui, people and chief of Ambaidiru village, Pak Makarius, George Argent, Andrew Ensoll, Sadie Barber and Herkilaus Rumaikewi. Financial support for the expedition was provided by the Royal Horticultural Society, the Merlin Trust, Royal Botanic Garden Edinburgh Members' Committee, Royal Botanic Garden (Sibbald) Trust and the James & Eve Bennett Charitable Trust.

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Publisher's Note

Appendix 4: Nishii, K., Kokubugata, G., Möller, M. & Atkins, H.J. 2019. Notes on *Cyrtandra* (Gesneriaceae) from Japan, Taiwan and Batan Island (Philippines). *Edinburgh Journal of Botany* 76(3): 333-344.

doi: 10.1017/S0960428619000106

NOTES ON *CYRTANDRA* (GESNERIACEAE) FROM JAPAN, TAIWAN AND BATAN ISLAND (PHILIPPINES)

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As part of ongoing molecular phylogenetic work on the large Gesneriaceae genus *Cyrtandra*, new insights into the taxonomy and relationships of the *Cyrtandra* of Japan, Taiwan and Batan Island in the northern Philippines have emerged. *Cyrtandra umbellifera* is confirmed as a species with a distribution that includes both Taiwan and Batan Island. *Cyrtandra yaeyamae* is found to be distinct from the widespread *C. cumingii*, with a distribution that includes both the Ryukyu Islands in Japan and Batan Island.

Keywords. Batan Island, *Cyrtandra*, Japan, lectotypification, Philippines, Taiwan, taxonomy.

INTRODUCTION

Cyrtandra J.R.Forst. & G.Forst. is the largest genus in the Gesneriaceae, with more than 800 species (Atkins *et al.*, 2013). Its distribution extends from the Nicobar Islands in the west, across the islands of Malesia to New Guinea, and across the Pacific to Hawaii. In continental Asia, the genus is distributed as far north as Phetchaburi in Thailand and reaches its most northern limit in Asia in Taiwan (Lanyu Island) and the Ryukyu Archipelago (hereafter the Ryukyus) of Japan, where it is represented by two species; in Taiwan by *Cyrtandra umbellifera* Merr. (Li & Kao, 1998), and in Japan by the widespread *C. cumingii* C.B.Clarke (Yamazaki, 1993) (Fig. 1).

TAXONOMIC HISTORY OF *CYRTANDRA* IN JAPAN AND TAIWAN

Taiwan

Cyrtandra umbellifera was first described by Merrill in 1908 from near the summit of Mount Iraya in Batan Island, Philippines (Merrill, 1908). In 1935, Hosokawa described *Cyrtandra kotoensis* Hosok. from Mount Hontou-shan (formerly Mount Koto-yama) on Lanyu Island in Taiwan and referred to it as being distinct from *C. umbellifera* by having leaves with oblique bases and much shorter subulate calyx lobes (Hosokawa, 1935). This was considered to be a synonym of *Cyrtandra umbellifera* (Kao & DeVol, 1972), and this was maintained in the most recent *Flora of Taiwan* (Li & Kao, 1998).

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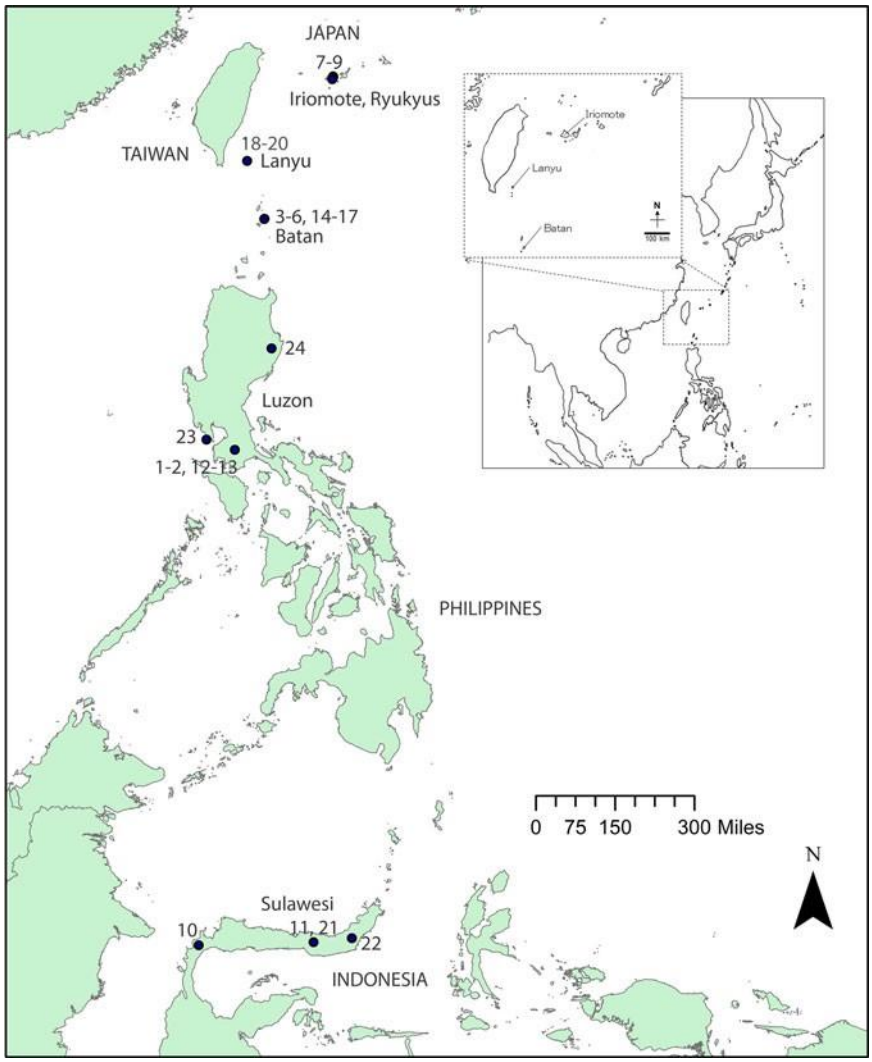

F I G . 1 . Map of localities of all samples included in the analysis. Numbers relate to the sample list in Table 1.

Japan

Cyrtandra cumingii is a large-leaved species with distinctive white bracts that was first described by Clarke in 1883 (Clarke, 1883) from two collections from Luzon in the Philippines. This species was later mentioned in a number of accounts of the Philippine flora by the American botanists Elmer and Merrill, in which it was described as being "widely distributed in the Philippines" (Merrill, 1907) and its distribution expanded to include Batan (Merrill, 1908), Luzon, Mindanao and Negros (Elmer, 1908); it was mentioned as being "especially common on Mt Banahao, the type locality" (Merrill, 1923).

In May 1937, a very similar-looking species was described from Iriomote Island, the southern Japanese island of the Ryukyus, and given the name *Cyrtandra yaeyamae* Ohwi and listed as being endemic to this island (Ohwi, 1937). No reference was made by Ohwi to the widespread Philippine species *Cyrtandra cumingii*. Just one month later, Masamune described another very similar-looking species from Iriomote in the Ryukyus and named it *Cyrtandra iriomotensis* Masam. (Masamune, 1937) and remarked that this was the first record of this widespread genus in Japan. This has subsequently always been treated as a synonym of *Cyrtandra yaeyamae* (Hatusima, 1956; Walker, 1976). In 1956, Hatusima listed *Cyrtandra yaeyamae* as a synonym of *C. cumingii*, but in 1971 he resurrected it as a variety of *C. cumingii* (Hatusima, 1956, 1971). Not long after, in 1973, Gillett, in his treatment of the *Cyrtandra* of the Caroline Islands and Ryukyus (Gillett, 1973), treated *C. yaeyamae* as a distinct species known only from Iriomote Island. Similarly, in 1976, in the *Flora of Okinawa and the Southern Ryukyu Islands*, Walker (1976) used the name *Cyrtandra yaeyamae* and stated that the Japanese species could be distinguished from the similar Philippine one by "having much smaller, narrower inflorescence-bracts and smaller indumentum-hairs, appearing less pubescent" and listed it as a Japanese endemic. Most recently, in the *Flora of Japan* (Yamazaki, 1993), *Cyrtandra yaeyamae* was sunk back into *C. cumingii* and listed as a widespread species from the Southern Ryukyus and the Philippines.

In this study, a stable phylogeny of the genus across Japan, Taiwan and the Philippines was generated, including the samples recently collected as *Cyrtandra cumingii* from the Ryukyus (Japan), Batan Island and Luzon (both from the Philippines) and *C. umbellifera* from Lanyu Island (Taiwan) and Batan Island (the Philippines), and we were able to test the relationships of these two species with their closest congeners to clarify their taxonomic status.

Materials and Methods

Taxon sampling

We sampled 13 recent collections of the focus taxa *Cyrtandra cumingii* and *C. umbellifera*, which had been made by one of the authors (G.K.), and one by S. Scott (Royal Botanic Garden Edinburgh), from the key localities of Batan Island in the Philippines, Iriomote Island in Japan, and Lanyu Island in Taiwan, and an earlier collection of *C. cumingii* from near the type locality in Luzon, the Philippines. These were added to a matrix containing a further five samples of closely related taxa from the Philippines selected from a large phylogeny of the genus across Southeast Asia (Atkins *et al.*, unpublished data). Four additional samples of *Cyrtandra* from Sulawesi in Indonesia were included as outgroup taxa based on unpublished results of work by Atkins and colleagues, giving a total of 24 accessions (Table 1; see Fig. 1).

DNA extraction

Total genomic DNA was extracted from fresh leaf material or silica-dried material using a modified CTAB procedure (Doyle & Doyle, 1987) or using the QIAxtractor (Qiagen,

T AB LE 1 . Taxon list for samples of *Cyrtandra* included in the present analysis

No.	Species	Origin	Collector and number	Voucher deposition
1	*C.* cf. *roseo-alba*	Philippines, Luzon	*QCB Cronk* MAK1	E
2	*C. cumingii*	Philippines, Luzon	*QCB Cronk* MAK5	E
3	*C. cumingii*	Philippines, Batan	*G Kokubugata* GK15782	TNS
4	*C. cumingii*	Philippines, Batan	*G Kokubugata* GK15794	TNS
5	*C. cumingii*	Philippines, Batan	*G Kokubugata* GK15861	TNS
6	*C. cumingii*	Philippines, Batan	*G Kokubugata* GK15867	TNS
7	*C. cumingii*	Japan, Ryukyus	*S. Scott* 500	E
8	*C. cumingii*	Japan, Ryukyus	*G Kokubugata* GK8701	TNS
9	*C. cumingii*	Japan, Ryukyus	*G Kokubugata* GK18916	TNS
10	*C. fasciata* H.J.Atkins	Indonesia, Sulawesi	*G Argent* et al. 198	E
11	*C. fasciata*	Indonesia, Sulawesi	*H Atkins* et al. 54	E
12	*C. incisa* C.B.Clarke	Philippines, Luzon	*QCB Cronk* MAK4	E
13	*C. lagunae* Kraenzl.	Philippines, Luzon	*QCB Cronk* MAK3	E
14	*C. umbellifera*	Philippines, Batan	*G Kokubugata* GK15792	TNS
15	*C. umbellifera*	Philippines, Batan	*G Kokubugata* GK15857	TNS
16	*C. umbellifera*	Philippines, Batan	*G Kokubugata* GK15859	TNS
17	*C. umbellifera*	Philippines, Batan	*G Kokubugata* GK15858	TNS
18	*C. umbellifera*	Taiwan, Lanyu Island	*G Kokubugata* GK6016	TNS
19	*C. umbellifera*	Taiwan, Lanyu Island	*G Kokubugata* GK6025	TNS
20	*C. umbellifera*	Taiwan, Lanyu Island	*G Kokubugata* GK6031	TNS
21	*C. serratifolia* H.J.Atkins	Indonesia, Sulawesi	*H Atkins* et al. 93	E
22	*C. serratifolia*	Indonesia, Sulawesi	*S Barber* et al. BAKK 44	E
23	*C.* sp	Philippines, Luzon	*S Scott* 501	E
24	*C.* sp.	Philippines, Luzon	*M Mendum* et al. 29009	E

Hilden, Germany). The primers used in this study are listed in Table 2. PCR was carried out with Biotaq DNA polymerase (Bioline, London) and with CES PCR enhancer (Ralser *et al.*, 2006) with the following chemical concentrations: 10× buffer, 1 μL; 20 mM dNTP, 1 μL; 50 mM $MgCl_2$, 0.3 μL; forward and reverse primers, 0.4 μL each; CES, 2 μL; Biotaq, 0.2 μL; DNA, 1–2 μL; with distilled H_2O added to make up 10 μL. PCR amplifications of internal transcribed spacer (ITS) and *mat*K were carried out with 94°C for 4 min, 35 cycles of 94°C for 1 min, 55°C for 1 min and 72°C for 1.5 min, followed by 72°C for 10 min; for *trn*L–F with 94°C for 4 min, 35 cycles of 94°C for 30 s, 57°C for 30 s and 72°C for 1 min, followed by 72°C for 10 min; for *psb*A–*trn*H and *rpl*32–*trn*L with 94°C for 4 min, 35 cycles of 94°C for 1 min, 52°C for 1 min and 72°C for 1.5 min, followed by 72°C for 10 min.

All PCR amplifications were carried out on a Bio-Rad Tetrad DNA Engine (Bio-Rad, Hercules, California). The PCR products were visualised under ultraviolet light after electrophoretic separation on a 1% agarose gel stained with SYBR Safe gel stain (Invitrogen, Carlsbad, California). PCR products were subsequently purified using Exo-SAP-IT (Thermo Fisher Scientific, Waltham, Massachusetts) following the manufacturer's protocol. Sequencing PCRs were carried out with BigDye Terminator version 3.1 Cycle

TABLE 2. Primers used for PCR and sequencing

Region	Name	Direction	Primer sequence	Reference
ITS	ITS_5P	Forward	GGA AGG AGA AGT CGT AAC AAG	Möller & Cronk (1997)
ITS	ITS_8P	Reverse	CAC GCT TCT CCA GAC TAC A	Möller & Cronk (1997)
*trn*LF	trnLcG	Forward	GTG AAG ACT TCT AAA TTC AGA GAA AC	The present study
*trn*LF	trnLf	Reverse	ATT TGA ACT GGT GAC ACG AG	Taberlet *et al*. (1991)
*psb*A–*trn*H	psbAf	Forward	GTT ATG CAT GAA CGT AAT GCT C	Sang *et al*. (1997)
*psb*A–*trn*H	trnHr	Reverse	CGC GCA TGG TGG ATT CAC AAA TC	Sang *et al*. (1997)
*rpl*32–*trn*L	rpl32-F	Forward	CAG TTC CAA AAA AAC GTA CTT C	Shaw *et al*. (2007)
*rpl*32–*trn*L	trnL$^{(UAG)}$	Reverse	CTG CTT CCT AAG AGC AGC GT	Shaw *et al*. (2007)
*mat*K	matK.206F	Forward	CCG GGT TAT GAC AAT AAA TCC AGT	Luna *et al*. (in press)
*mat*K	matK.946R	Reverse	ATA AAT CCT TCT TGG ATG AAA CCA C	Luna *et al*. (in press)
*mat*K	matK.cy2F	Forward	TGG CAA TGG CAT TTT TCG CT	The present study
matK	matK.1734R	Reverse	CCG TGC TTG CAT TTT TCA TTG C	Luna *et al*. (in press)

ITS, internal transcribed spacer.

Sequencing Kit (Applied Biosystems, Foster City, California) following the manufacturer's protocol, and the same primers used for PCR amplification. Sequencing was carried out by Edinburgh Genomics at the University of Edinburgh. The resulting electropherograms were combined and edited in Sequencher version 5.1 (Gene Codes Corporation, Ann Arbor, Michigan) and a matrix assembled, aligned and manually adjusted in Bioedit version 7.1.11 (Hall, 1999).

Phylogenetic analyses

Maximum parsimony (MP) analyses were initially conducted on individual regions to visually assess congruence, with areas of conflict determined by examining the placement of individual taxa on each gene tree. Relationships were considered incongruent if the placement of taxa varied among the individual gene trees and exhibited MP-BS values > 80%. No significant incongruence was present, so all further phylogenetic analyses were carried out on the combined data set.

Maximum parsimony analyses were carried out using PAUP version 4.0a163 (Swofford, 2002) on unweighted and unordered characters. Alignment gaps were treated as missing data.

A full heuristic search was carried out using stepwise random addition of 10,000 replicates, with TBR and Multrees on. Statistical branch support was obtained from 10,000 heuristic bootstrap replicates each starting with a random addition tree, optimised with TBR on and Multrees off. Bayesian inference (BI) phylogenetic analyses were carried out using Mr Bayes version 3.2.6 (Ronquist *et al*., 2012). The data were divided into seven partitions (ITS spacers, 5.8S gene, *psb*A–*trn*H, *rpl*32–*trn*L, *trn*L–F, *mat*K coding region, *mat*K intron region), analysed under the best-fit model of nucleotide evolution for each genic region selected using the AIC criterion as implemented in MrModeltest version 2.4 (Nylander, 2004). These were GTR+G for the ITS spacers, *trn*L–F, *psb*A–*trn*H and the *mat*K intron region, GTR+I+G for *rpl*32–*trn*L and the *mat*K coding region, and SYM+I for the ITS 5.8S gene.

Two runs with four chains each were run for 1,000,000 generations with a tree sampled every 1000th generation, and convergence between the runs was checked in Tracer version 1.7 (Rambaut *et al*., 2018). The first 10% of sampled trees were discarded as burn-in and the remainder summarised as a maximum clade credibility tree and posterior probabilities (PP) extracted. Maximum likelihood (ML) analyses were conducted with RAxML version 8 (Stamatakis, 2014) via the CIPRES Gateway (Miller *et al*., 2010). The search for the optimal ML tree was performed using GTR+I+G and a rapid bootstrap analysis of 1000 replicates. For the ML and Bayesian analyses, tree topology and node support were examined in FigTree version 1.4.3 (Rambaut, 2007).

Results

Our results (Fig. 2) show that the three *Cyrtandra umbellifera* collections from Taiwan form a strongly supported clade (BI-PP = 1, ML-BS = 96%, MP-BS = 89%), in a maximally supported sister relationship to a clade of four samples of the same species from Batan Island in the Philippines (BI-PP = 1, ML-BS = 97%, MP-BS = 83%). These together were sister to an unidentified sample from Luzon with strong support (BI-PP = 1, ML-BS = 99%, MP-BS = 98%). The collections of *Cyrtandra cumingii* from Batan Island and Japan were mixed together in a clade that received maximum branch support (BI-PP = 1, ML-BS = 100%, MP-BS = 100%).

The single sample of *Cyrtandra cumingii* from Luzon was, however, in a well-supported sister relationship with *C.* cf. *roseo-alba*, also from Luzon, with maximum branch support (BI-PP = 1, ML-BS = 100%, MP-BS = 100%), that was weakly associated (BI-PP = 0.71, ML-BS = 56%, MP-BS = 52%) with another clade.

Discussion

Cyrtandra umbellifera

The results for *Cyrtandra umbellifera* suggest that the species on Taiwan could be either separated as a distinct species from the Philippine collections or kept together as a species with a distribution that includes both the Philippines and Taiwan. Our observations of the morphology suggest that it is not possible to separate these two, and that the morphological

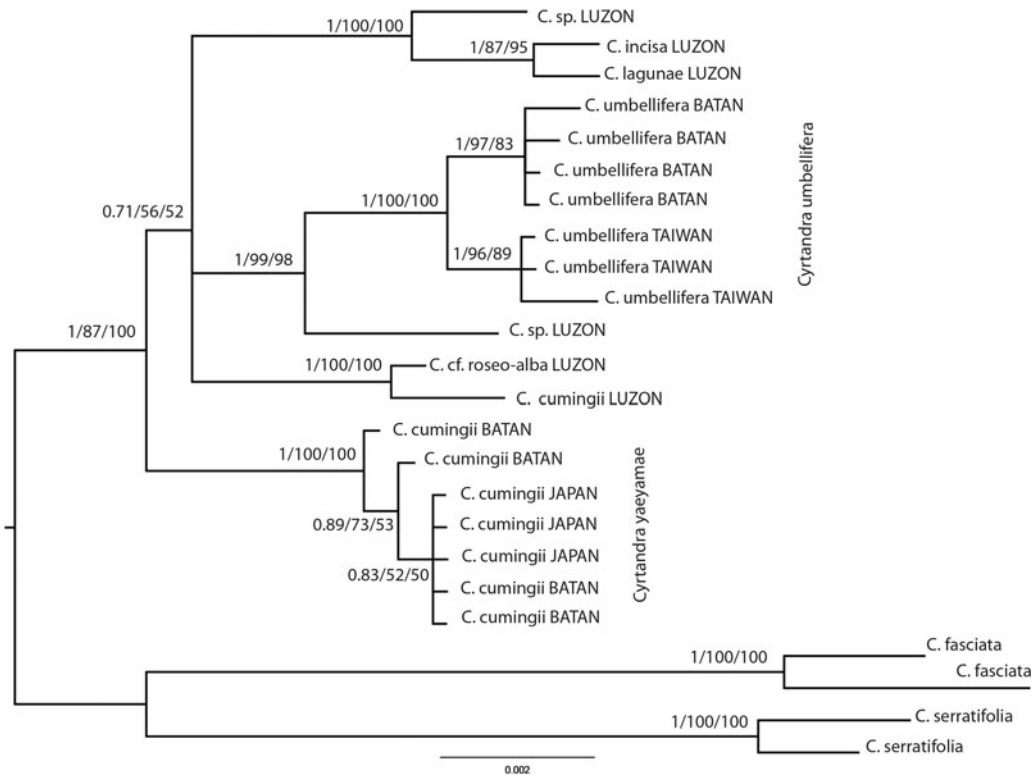

FIG. 2. Bayesian inference tree based on combined sequences of ITS, *psb*A–*trn*H, *rpl*32–*trn*L, *trn*L–F and *mat*K. Node support is indicated as Bayesian posterior probabilities (BI-PP), maximum likelihood bootstrap support (ML-BS) and maximum parsimony bootstrap support (MP-BS).

differences suggested by Hosokawa (1935) to differentiate *Cyrtandra kotoensis* (i.e. leaves with oblique bases and much shorter subulate calyx lobes) are not consistent.

Cyrtandra cumingii

Our phylogenetic results show that the collections from Japan are not *Cyrtandra cumingii*. This had been suggested previously by a number of authors (Ohwi, 1937; Gillett, 1973; Walker, 1976), although they had also stated that the species present on Iriomote Island of the Ryukyus was endemic. What these results show is that the species present in Iriomote Island of the Ryukyus is also present in the northern Philippines. This had not been suggested by earlier authors. On inspection of the specimens from the northern Philippines and Japan, there do appear to be good, consistent differences between these and the type of *Cyrtandra cumingii* from southern Luzon. These include differences in the number of lateral veins (15–18 in *Cyrtandra yaeyamae* and 12 in *C. cumingii*), calyx length (12–15 mm in *C. cumingii* and 5–6 mm in *C. yaeyamae*), and also leaf bases (often distinctly decurrent in *C. yaeyamae*, not in *C. cumingii*). There may be additional floral differences once a detailed revision of *Cyrtandra cumingii* in the Philippines can be carried

out, because no corolla was seen or described by Clarke (1883). The specimen from Batan Island cited as being *Cyrtandra cumingii* (*Fenix* 3787, US 00081311) (Merrill, 1908) and the justification for the expansion of its distribution to this island is, in fact, a close match for the other specimens included in this analysis from Batan Island and not a good match for the type collection of *C. cumingii* from Luzon.

In future studies, more intensive sampling across the rest of the Philippines would be useful, as well as a detailed study of morphology to determine the extent of the distribution of *Cyrtandra yaeyamae* and *C. cumingii* in the Philippines.

Taxonomic Implications

Cyrtandra cumingii C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 263 (1883). – Type: Philippines, Luzon, 1841, *Cuming* 757 (lecto K [K000831609]; isolecto K [K000831610], P [P03884307], BM [BM000798277] hic. desig.).

Distribution. Philippines (Luzon, Mindanao, Mindoro, Panay).

This appears to be a fairly common and widespread species in Luzon, with a few records also from Mindanao, Panay and Mindoro. More intensive sampling and taxonomic work are required in the Philippines to determine the exact distribution and limits of this species. The name *Cyrtandra cumingii* has not been lectotypified, so we do that here, selecting the most complete specimen at Kew (K000831609) as the lectotype.

Cyrtandra umbellifera Merr. in Philipp. J. Sci. 3: 435 (1909 ["1908"]). – Type: Batan Island, Philippines, 8 vi 1907, *Fenix* 3785 (lecto P [P03899661], isolecto US [US00126364] hic. desig.). Fig. 3.

Cyrtandra kotoensis Hosokawa in Trans. Nat. Hist. Soc. Formosa 25: 412 (1935). – Type: Taiwan, Island of Botel Tobago, Mt Koto, 7 xii 1935, *Hosokawa* 8129 (holo TAI).

Distribution. Taiwan and Batan Island, Philippines.

This distinctive species is characterised by its umbellate inflorescence and appears morphologically to be close to a number of species in the Philippines and Sulawesi that include *Cyrtandra longirostris* De Vriese, *C. callicarpifolia* Elmer and *C. bruteliana* Koord. from C.B.Clarke's section *Cuneatae*.

Merrill did not specify a herbarium when designating *Fenix* 3785 as the type for this species (Merrill, 1908), and it has not been possible to find any subsequent lectotypification. The collection from Paris (P03899661) is selected here as the lectotype.

Cyrtandra yaeyamae Ohwi in J. Jap. Bot. 13: 339 (1937). – "*Cyrtandra cumingii* var. *yaeyamae*" (Ohwi) Hatusima Fl. Ryukyus 557 (1971) ('*yaeyamana*') (not validly published; basionym cited only as "*C. yaeyamana* Ohwi (May 1937)", cf. Art. 41.5). – Type: Japan, Iriomote Island, Nakara-gawa, x 1936, *Sonohara s.n*. (holo KYO [KYO00069674]). Fig. 4.

Cyrtandra iriomotensis Masam., Not. Syst. 6: 38 (1937). – Type: Japan, Iriomote Island, *Masamune s.n*. (holo TAI [Herbar. Taihoku Imp. University] n.v.).

Cyrtandra cumingii auct. non C.B.Clarke; Hatusima (1956); Yamazaki (1993).

Distribution. Iriomote Island of the Ryukyus, Japan and Batan Island, Philippines.

FIG. 3 . *Cyrtandra umbellifera* Merr. A, Flower; B, habit; C, flower and fruits; D, habit. (Photographs: Goro Kokubugata; A and B, Lanyu, Taiwan; C and D, Batan Island, Philippines.)

Chromosome number. 2n = 34 (Kokubugata & Madulid, 2000).

This species is morphologically similar to the Philippine *Cyrtandra cumingii* but can be distinguished by the number of lateral veins (15–18 in *C. yaeyamae* and 12 in *C. cumingii*), calyx length (12–15 mm in *C. cumingii* and 5–6 mm in *C. yaeyamae*) and also often leaf bases (usually distinctly decurrent in *C. yaeyamae*, not in *C. cumingii*). The type of *Cyrtandra iriomotensis* has unfortunately not been seen. The type is cited as being at the Herbarium of Taihoku Imperial University in the protologue (Masamune, 1937). This became the Herbarium of the National Taiwan University (TAI) in 1945. Masamune was based in Taiwan throughout the Second World War and returned to Japan in 1945 (National Museum of Natural Sciences n.d.) with some of his collections, including a number of orchid types (Inoue *et al*., 1998) and potentially other types, as a number of his specimens cited as being at TAI have not been found there (Inoue *et al*., 1998). On returning to Japan, his collections were kept primarily at his home, and following his death, moved to the herbarium of Kanagawa Prefectural Museum of Natural History (KPM) (Inoue *et al*., 1998).

Despite efforts made to locate the type of *Cyrtandra iriomotensis* at TAI and KPM and other likely herbaria in Taiwan and Japan (HAST, KANA, KYO, RYU, TAIF, TI and

FIG. 4 . *Cyrtandra yaeyamae* Ohwi. A, Inflorescence; B, habit; C, inflorescence; D, habit. (Photographs: Goro Kokubugata; A and B, Batan Island, Philippines; C and D, Iriomote, Japan.)

TNS), we were unable to do so. Nonetheless, we are certain that this is conspecific with *Cyrtandra yaeyamae*, because the description of *C. iriomotensis* is a good match for the type of *C. yaeyamae* and, based on recent comprehensive fieldwork on Iriomote (area = 289.3 km^2) by one of the authors (G.K.), we are confident that there is only one species of *Cyrtandra* present on the island.

ACKNOWLEDGEMENTS

We would like to thank RBG Kew (K) for access to the collections and Gemma Bramley for her assistance during the visit. We would also like to thank Chien-Fan Chen (TAIF), Yi-Ru Cheng (TAI), Kunihiko Ueda (KANA), Wataru Ohnishi (KPM), Hidetoshi Nagamasu (KYO), Masatsugu Yokota (RYU) and Luisito Evangelista (PNH) for checking for type material. We would like to thank Mark Coode and John McNeil for their nomenclatural advice. We would also like to thank the Sibbald Trust for their contribution towards the project (Sibbald Project 2015#30). The Royal Botanic Garden Edinburgh is supported by the Rural and Environment Science and Analytical Services Division of the Scottish Government.

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Received 12 December 2018; accepted for publication 6 March 2019; first published online 20 May 2019

Appendix 5: Kartonegoro, A., Bone, R. & Atkins, H.J. 2018. Eleven new species of *Cyrtandra* (Gesneriaceae) from Sulawesi, Indonesia. *Edinburgh Journal of Botany* 75(2):173-204

doi: 10.1017/S0960428618000045

ELEVEN NEW SPECIES OF *CYRTANDRA* (GESNERIACEAE) FROM SULAWESI, INDONESIA

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Eleven new species of *Cyrtandra* (Gesneriaceae) from Sulawesi are described and illustrated: *C. albiflora* Karton. & H.J.Atkins, *C. boliohutensis* Karton. & H.J.Atkins, *C. gambutensis* Karton. & H.J.Atkins, *C. hekensis* Karton. & H.J.Atkins, *C. hendrianii* Karton. & H.J.Atkins, *C. hispidula* Karton. & H.J.Atkins, *C. kinhoii* Karton. & H.J.Atkins, *C. multinervis* Karton. & R.Bone, *C. nitida* Karton. & H.J.Atkins, *C. rantemarioensis* Karton. & R.Bone and *C. rubribracteata* Karton. & H.J.Atkins. Illustrations, maps and preliminary conservation assessments are provided for all the species.

Keywords. Cyrtandra, Gesneriaceae, new species, Sulawesi.

Introduction

Cyrtandra J.R.Forst. & G.Forst. is a large genus of c.800 species of herbs, shrubs, climbers and small trees (Atkins *et al.*, 2013). It is a predominantly Southeast Asian genus and is found in the Nicobar Islands in the Indian Ocean, throughout Malesia, in Taiwan and the southern Japanese islands, in northern Australia, and across the Pacific as far east as the Marquesas and north to Hawaii. It is recorded on the Asian continent only as far north as central Thailand. Its centres of diversity are New Guinea and Borneo (each with more than 100 species) and the Philippines (with more than 80 species) (Atkins *et al.*, 2013). It is found in the rain forest, from sea level to over 2000 m.

The Indonesian island of Sulawesi is the largest island in the biogeographical region known as Wallacea; it was identified in 2001 as being one of the top ten places in the world most in need of floristic work (Frodin, 2001), and it remains one of the islands in the region with the lowest collecting densities (Kessler *et al.*, 2002; Cannon *et al.*, 2007). The position of Sulawesi at the heart of Malesia, one of the most geologically complex areas in the world, makes knowledge of the affinities of the flora of the island crucially important to understanding both the biogeography of Southeast Asia and the evolution of many Southeast Asian plant groups (Mendum & Atkins, 2004).

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There is currently no revision of the genus *Cyrtandra* on Sulawesi, and until recently, no new taxa had been described since 1906. Recent expeditions to the island and subsequent research on the collections has, however, resulted in the description of a number of new species in the genus (Atkins, 2003; Bone & Atkins, 2013; Kartonegoro & Potter, 2014). The discovery of a further eleven new species, described here, brings the current total for the island to 32. More, however, await description, and a full revision, including a key and discussion on relationships and species groupings, based on ongoing molecular phylogenetic work on the genus in Southeast Asia, is in preparation.

Materials and Methods

All available *Cyrtandra* specimens from A, BM, BO, CANB, E, K, L, S and SING were examined. In addition, photographs of plants growing in the field and living collections held at the Royal Botanic Garden Edinburgh (RBGE) were consulted, when available. All vegetative and fruit measurements were taken from dried material and floral characters and measurements were taken from spirit material or rehydrated herbarium material. Species descriptions follow, as closely as possible, the structure and content of other published *Cyrtandra* descriptions from the island. A lack of collecting activity in Sulawesi, compared with other Indonesian islands (Cannon *et al.*, 2007), means that little material is available for comparison. All material cited (as type material and, when available, additional specimens) comprise the extent of our knowledge of these species.

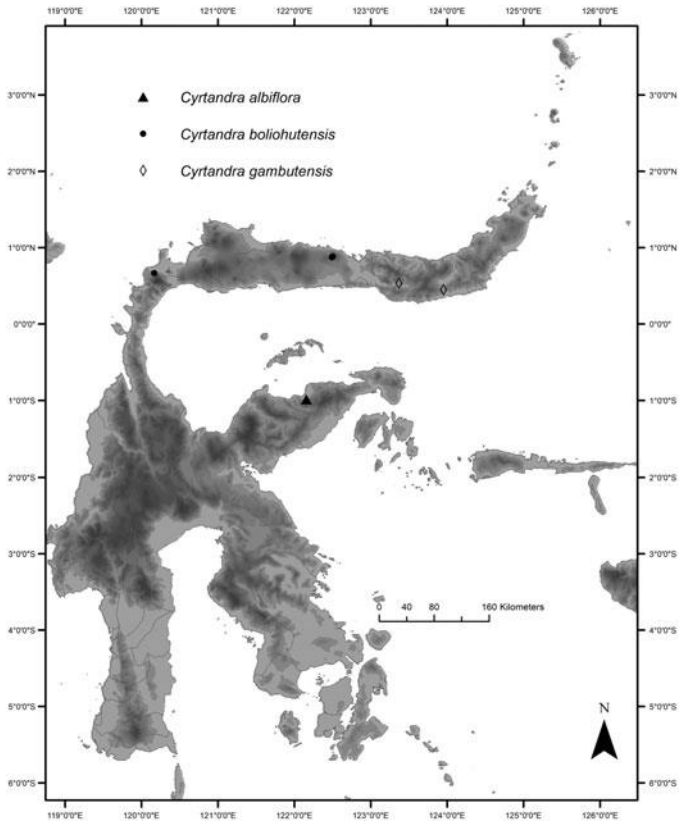
Proposals for IUCN conservation categories were made following the IUCN *Red List Categories and Criteria* and associated guidelines (IUCN, 2012). Forest types referred to in these notes follow the definitions stated in Cannon *et al.* (2007). When more than two collection localities were known for a species, precise geographical coordinates of collection localities from specimen labels, or georeferenced place names, were used to estimate extent of occurrence (EOO) and area of occupancy (AOO; *sensu* IUCN criterion B1) using a 2 km by 2 km grid cell in GeoCAT (Bachman *et al.*, 2011). Because Sulawesi is under-explored (and these species under-sampled), these calculations probably underestimate true EOO and AOO values; however, we feel that their inclusion helps to emphasise the urgent need for more extensive surveying in the region to adequately assess threats to these species.

Species Descriptions

The inflorescences of all the species described here are cymose, sometimes densely clustered and occasionally reduced to one or two flowers. Likewise, the fruits of all species are indehiscent.

Cyrtandra albiflora Karton. & H.J.Atkins **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its dense, villous indumentum, small white flowers and clustered axillary inflorescences. – Type:



Fi g. 1 . Known distribution of *Cyrtandra albiflora* Karton. & H.J.Atkins, *Cyrtandra boliohutensis* Karton. & H.J.Atkins and *Cyrtandra gambutensis* Karton. & H.J.Atkins.

Indonesia, Central Sulawesi, Sumber Agung, Sungai Spa, 92 m, 24 ii 2004, *Hendrian, Newman, Scott, Saleh & Supriadi* 848 (holo E, iso BO). **Figs 1, 2**.

Shrub up to 60 cm in height. *Stems* striate, densely villose hairy on young growth, hairs up to 3 mm, indumentum less dense on older growth. *Leaves* opposite, subequal (with occasional whorl of smaller leaves on cultivated plant); petiole c.2 cm long, hairy, narrowly winged; blades 17–22.5 × 5.1–7.7 cm, narrow oblong, apex acuminate, base attenuate, margin serrulate; 9–11 pairs of lateral veins and reticulate tertiary venation, light green and hairy above, appearing whitish and hairy below, most densely so on midrib and veins. *Inflorescences* axillary, subsessile, with c.8–10 flowers at various stages of development; bracts green, 10–11 × 5 mm, linear-lanceolate, hairy on both surfaces, most densely so along margins, caducous; bracteoles 6–8 mm long, linear, hairy internally and along margins; pedicels 2–3 mm long, densely hairy. *Calyx* tubular, green, 5–6 mm long, lower lip bilobed, lobes short acuminate, c.3 mm long, upper lip divided very briefly at apex, densely hairy externally. *Corolla* white, 10–12 mm

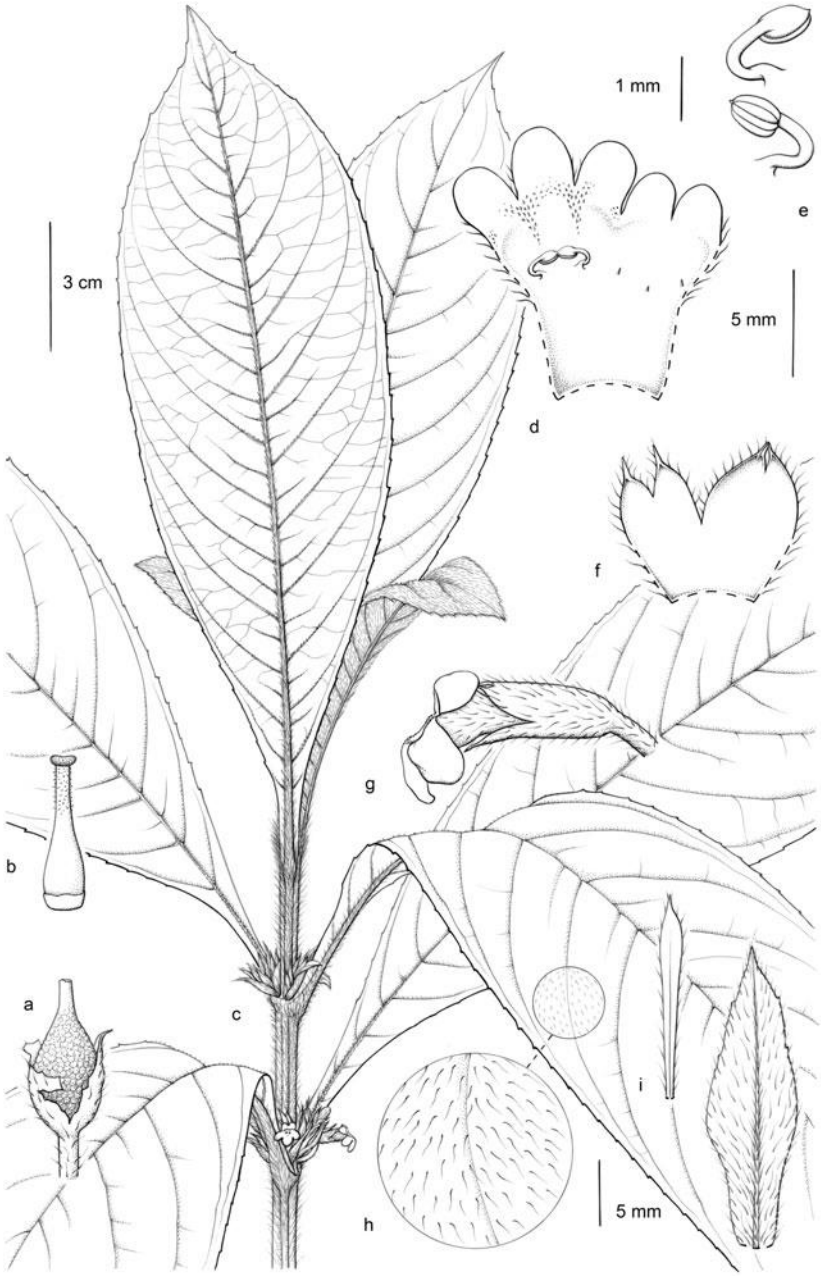


Fig. 2 . *Cyrtandra albiflora* Karton. & H.J.Atkins, sp. nov. A, Fruit enclosed by the persistent calyx; B, gynoecium; C, habit; D, corolla, longitudinal section; E, anthers; F, calyx, longitudinal section; G, flower, lateral view; H, detail of upper leaf surface; I, bracts and bracteoles. Drawn from *Hendrian* et al. 848 (E).

long, widening gradually to mouth, mouth oblique, upper lobes suborbicular, erect to slightly recurved, 1.5 × 2 mm, lower and lateral lobes more elongate, spreading to slightly recurved, 3 × 2.5 mm, hairy externally and with glandular hairs on inside of lobes and in mouth. *Stamens* 2; filaments short, c.1 mm long, attached 5–6 mm from base of corolla, glabrous; anthers c.1 mm long, glabrous, cohering at apices; staminodes 3, tiny, less than 0.2 mm long. *Gynoecium* 5.5–6 mm long overall; disc cupular with undulate margin, 1 mm long, glabrous; ovary glabrous; style glandular hairy; stigma slightly bilobed, lobes small and held upright on specimens seen. *Fruits* ovoid, drying dark brown, glabrous, verrucose, 5–6 × 2–3 mm, base of style and calyx persistent.

Distribution. Central Sulawesi: Luwuk (see Fig. 1).

Habitat and ecology. Disturbed lowland primary forest in a limestone area at an altitude of 92–220 m.

Etymology. This species is named for its white flowers.

Proposed IUCN conservation category. Cyrtandra albiflora is known from a single mountain from two collections made on the same trip in 2004 at altitudes of 92 and 220 m from disturbed primary forest in a limestone area. According to Cannon *et al.* (2007), "little over 20% of lowland forests" can be described as "good forest cover" in Sulawesi, and it is one of the most threatened habitats on the island. There are no protected areas in this part of Sulawesi (UNEP-WCMC & IUCN, 2016).

A lack of specimens of *Cyrtandra albiflora* precludes estimations of EOO and AOO. Until more intensive botanical exploration can be made in this area, it is assumed that this species is restricted to the type locality. It is not possible to comment on latent threats to the population with any certainty, but if the general threats to this habitat type are real (specifically forest clearance for agriculture) and there is no protection in place, then the only known population of this species could be at risk of decline or extinction. We recommend that this species is categorised as Vulnerable (VU) using the criterion VUD2, because it is a population with a very restricted number of locations and, as such, is prone to the effects of human activities or stochastic events and thus capable of becoming Critically Endangered or even Extinct in a short period of time, and we emphasise the importance of carrying out further survey work in this region.

Additional specimen examined. **Central Sulawesi**: Luwuk, Mt Hek, Sungai Spa, 24 ii 2004, *Scott, S.* 04–307, grown on at RBGE as accession 20040645A, vouchered as *Scott* 509 (E).

This species is most similar to *Cyrtandra hendrianii* (described here and collected from the same location), but it can be distinguished by its white corolla (versus corolla pink), green calyx (versus calyx red), densely villous stems and leaves (versus stems and leaves more less glabrous) and linear-lanceolate bracts 10–11 mm long (versus oblong-lanceolate bracts, 25–35 mm long).

Cyrtandra boliohutensis Karton. & H.J.Atkins **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its inflorescence at the base of the stem, anisophyllous leaves and ridged calyx. – Type: Indonesia, Gorontalo Province, Mt Boliohutu, 300 m, 24 iv 2002, *Atkins, Mendum, Newman, Hendrian & Sofyan* 188 (holo BO, iso E). **Figs 1, 3**.

Branching herb up to 1 m in height. *Stems* slender, striate, sparsely hairy. *Leaves* opposite, both members of a pair well developed but somewhat unequal in size or with one leaf of a pair markedly reduced, sometimes appearing alternate; petioles 1.2–2.5 cm long, hairy; blades 7–14 × 3–5 cm, oblong to narrow oblong, occasionally somewhat rhomboid, apex acuminate, base attenuate, slightly asymmetrical, margin serrate; 4–6 pairs of lateral veins, curving and running eventually out to margin, subglabrous above, sparsely hairy below, more densely so on midrib and veins; reduced leaves (where present) 4–5 mm long, scale-like, occasionally cordate. *Inflorescences* subsessile to shortly pedunculate in leaf axils or at base of stems in the axils of fallen leaves, 1- or 2-flowered; peduncle 1–2 mm long, hairy; bracts elliptic or oblong, glabrous, greenish brown, 11–22 × 8–10 mm, partly enclosing calyx at the base, bilobed at apex or divided almost to base, sparsely hairy; bracteoles single, oblong, glabrous, green-brown, 10–16 × 5–6 mm; pedicels 2–5 mm long, sparsely hairy. *Calyx* tubular, ridged, green becoming dark red along ridges, 17–25 mm long, evenly 5-lobed, lobes 2 mm long, triangular, acuminate at apex, sparsely hairy outside. *Corolla* white, tube somewhat flushed pinkish outside, yellow in throat with fine, purple spots on the inside of lobes, 35–65 mm long, narrowly funnel-shaped, flattened laterally, brown hairy externally, lobes spreading not recurved, 9–10 × 5–8 mm. *Stamens* 2; filaments 8– 12 mm long, attached 20–30 mm above base of corolla; anthers 1.5–3 mm long, thecae more or less parallel, coherent at apices, with a 'fringe' of hairs at the base of each anther; staminodes 3, 4–7 mm long. *Gynoecium* 23–35 mm long overall; disc cupular with lobed margin, 2 mm, glabrous; ovary glabrous; style glabrous at base, eglandular hairy towards stigma; stigma peltate, slightly bilobed, 2 mm across. *Fruits* cylindrical to narrow ovoid or elongate, green or brown-green, glabrous, verrucose, 10–25 × 2–4 mm; calyx not or only partially persistent, base of style persistent.

Distribution. Gorontalo and Central Sulawesi (see Fig. 1).

Habitat and ecology. Lowland to lower montane forest at an altitude of 300–1400 m.

Etymology. This new species is named after one of the mountains on which it was collected.

Proposed IUCN conservation category. Based on both the EOO and AOO, this species would be in the Critically Endangered category (based on 2 × 2 km grid cell size) under the B criteria (Bachman *et al.*, 2011). The three collections do, however, fall within the protected areas of Nantu Sanctuary Forest and Mount Sojol Nature Reserve (UNEP-WCMC & IUCN, 2016), but at relatively low altitudes, of approximately 300 m, where the general threat to this habitat type on the island is known to be high (Cannon *et al.*,

2007; Thomas *et al*., 2011). Given the restricted distribution of this species and the uncertainty about threat, we recommend Vulnerable (VU) for this species, using the criterion VUD2, and reiterate the need for further botanical exploration in the area.

Additional specimens examined. **Gorontalo**: Mt Boliohutu, 320 m, 24 iv 2002, *Atkins* et al. 190 (E, L); Mt Boliohutu, 320 m, 24 iv 2002, *Scott, S.* 02–126, grown at RBGE as accession 20021906A, vouchered as *Scott* 505. **Central Sulawesi**: Mt Sojol, 1400 m, 27 ii 2000, *Mendum* et al. 00196 (E, L).

This species appears to be morphologically similar to a group of Bornean species that include *Cyrtandra basiflora* C.B.Clarke. They all have large flowers with long, soft hairs, flower at the base of the stem, have slightly rhomboid, anisophyllous leaves and have a ridged calyx. Of the Bornean species in this group (which includes *Cyrtandra sandakanensis* B.L.Burtt, *Cyrtandra simplex* Merr., *Cyrtandra sublanea* Hilliard & B.L.Burtt and *Cyrtandra tenebrosa* B.L.Burtt), *C. boliohutensis* is morphologically most similar to *C. basiflora* from Sarawak and Brunei but can be most easily distinguished from this species by the number of flowers in the inflorescence (1- or 2-flowered in *C. boliohutensis* versus 6- or 7-flowered in *C. basiflora*).

Mendum et al. 00196 from Mount Sojol has been included here, although there are some differences in the shape of the inflorescence bracts. Two further collections from Lore Lindu National Park in Central Sulawesi, *Cicuzza* 549 and 984, are similar to this species but do not have the distinctive thick beard of hairs at the base of the anthers. Further collections are required to clarify the status of these two collections.

Cyrtandra gambutensis Karton. & H.J.Atkins **sp. nov.**

Distinguished from *Cyrtandra engleri* Koord. by its obscure tertiary venation (versus tertiary venation visible), 8–11 secondary veins (versus 4 or 5 secondary veins) and anthers glabrous (versus anthers with a tuft of hairs at apex). – Type: Indonesia, Gorontalo Province, Mt Gambuta, 520 m, 8 iv 2002, *Atkins, Mendum, Newman, Hendrian & Sofyan* 38 (holo E, iso BO). **Figs 1, 4**

Shrub 0.7–2.5 m. *Stems* striate, short hairy, appearing pubescent. *Leaves* opposite, unequal; one leaf of a pair markedly reduced; petioles 0.8–1.3 cm long, hairy; blades 6–9.5 × 1–2.5 cm, oblanceolate, apex short acuminate, acumen 4–5 mm long, base attenuate, slightly asymmetrical, margins subentire; 8–11 pairs of lateral veins running straight out to margin, sparse tertiary venation, glabrous above, hairy below, most densely so on midrib, veins and margin; reduced leaves cordate, 5 × 4 mm, resembling the larger leaves in other respects. *Inflorescences* axillary, sessile, 2- or 3-flowered; bracts oblong-lanceolate, 5 × 1 mm, hairy on both sides; bracteoles lanceolate, hairy, 3–4 × 0.5 mm; pedicels 3–5 mm long, densely hairy. *Calyx* tubular, white, green in bud, c.15 mm long, densely hairy externally, three upper lobes c.7 mm long, acuminate, two lower lobes c.8 mm long triangular, acuminate at apex. *Corolla* white with purple markings on lobes, tube narrow in basal third, widening to mouth in apical two-thirds, 19–20 mm long, densely hairy externally, upper lobes suborbicular, 4 × 2 mm, lower and lateral lobes ovate, 5 × 3 mm. *Stamens* 2; filaments 5 mm long, attached 8 mm

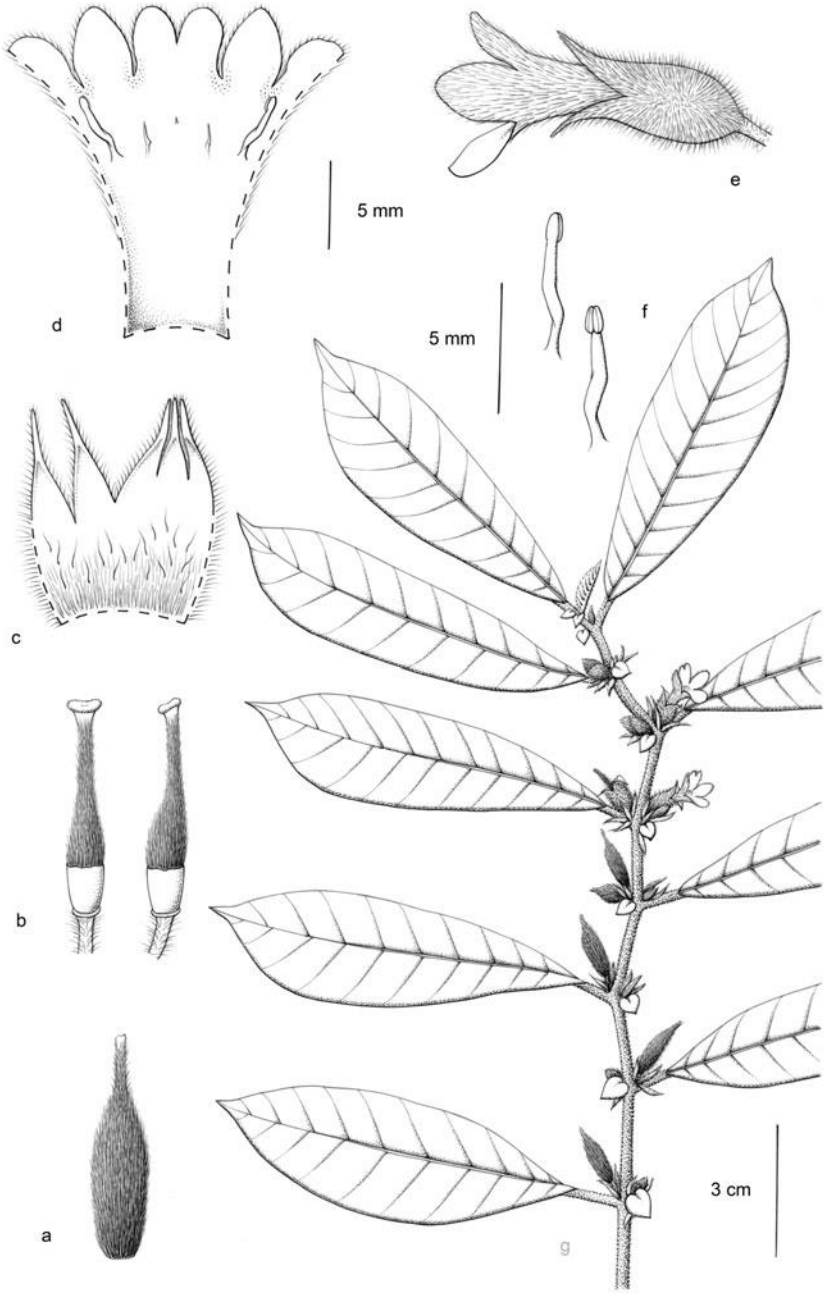


Fig. 4. *Cyrtandra gambutensis* Karton. & H.J.Atkins, sp. nov. A, Fruit; B, gynoecium; C, calyx, longitudinal section; D, corolla, longitudinal section; E, flower, lateral view; F, stamens; G, habit. Drawn from *Atkins* et al. 38 (E).

above base of corolla, white; anthers 1 mm long, thecae parallel, not coherent at apices, purple; staminodes 3, c.2 mm long. *Gynoecium* c.11 mm overall; disc cupular with undulate, fringed margin, glabrous externally, 2 mm long; ovary and style densely eglandular hairy; stigma bilobed, 2 mm across. *Fruits* elongate, dark green, cylindrical, densely hairy, 9 × 3 mm; calyx not persistent, base of style persistent.

Distribution. North Sulawesi and Gorontalo (see Fig. 1).

Habitat and ecology. Lowland to lower montane forest at an altitude of 520–950 m.

Etymology. Named after the mountain on which the type was collected.

Proposed IUCN conservation category. Cyrtandra gambutensis is known from two collections made in 1985 and 2002 at relatively low altitude in disturbed primary rain forest within the Bogani Nani Wartabone National Park. The National Park status should provide some protection, although "deforestation for the production of crops like cloves, palm oil and coffee" is considered to be a threat in this area (Rainforest Trust, no date). A lack of specimens precludes estimations of EOO and AOO, so we recommend that this species is categorised as Vulnerable (VU) using the criterion VUD2, because it is a population with a very restricted AOO or number of locations and, as such, is prone to the effects of human activities or stochastic events and is thus capable of becoming Critically Endangered or even Extinct in a short period of time, and emphasise the importance of carrying out further survey work in this region.

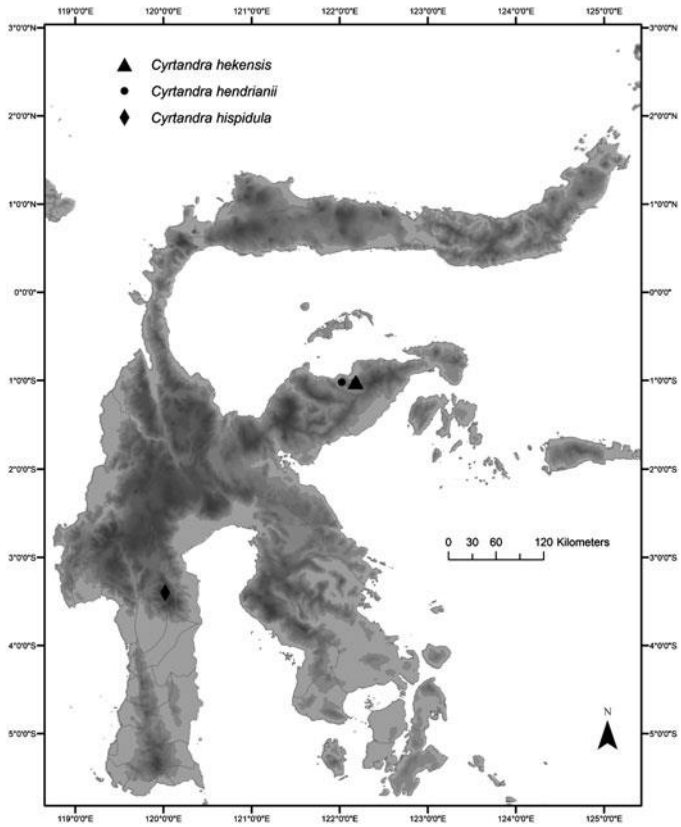
Additional specimen examined. **North Sulawesi**: Bolaang Mongondow, Dumoga Bone National Park, G. Mogogonipa, 10 iv 1985, *de Vogel & Vermeulen* 7081 (L).

This species is part of a group of apparently closely related species in Sulawesi that share the characteristics of strongly anisophyllous leaves (wherein the smaller leaf is highly reduced), white corollas and densely hairy calyces, corollas and fruits. The other species in the group are *Cyrtandra engleri* Koord., *Cyrtandra gorontaloensis* H.J.Atkins and *Cyrtandra widjajae* Karton. *Cyrtandra gambutensis* can be distinguished from the others by its narrow leaves, sparse tertiary venation and numerous secondary veins that run straight out to the margin without looping upwards.

Cyrtandra hekensis Karton. & H.J.Atkins **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its coarse indumentum, serrate leaves and white flowers with greenish yellow markings in throat. – Type: Indonesia, Central Sulawesi, Mt Hek, 420 m, 9 iv 2008, *Thomas, D.C. & Ardi, W.H.* 08–26 (holo BO, iso E). **Figs 5, 6**.

Herb up to 25 cm in height. *Stems* ridged, striate, upper stem appearing reddish, from dense, coarse indumentum on young growth, older stems glabrous. *Leaves* opposite, slightly unequal; those of a pair well developed but one slightly smaller; petioles 0.8–2 cm long, densely coarse hairy on young growth becoming glabrous on older growth, narrowly winged; blades 7–7.5 × 1.6–3 cm (larger leaves), 3.5–5 × 1.3–1.7 cm (smaller leaves), narrow elliptic or oblong to somewhat oblanceolate, apex acuminate, base



Fi g. 5 . Known distribution of *Cyrtandra hekensis* Karton. & H.J.Atkins, *Cyrtandra hendrianii* Karton. & H.J.Atkins and *Cyrtandra hispidula* Karton. & H.J.Atkins.

attenuate, margin serrate; 4–6 pairs of lateral veins and reticulate tertiary venation; dark green and mostly glabrous above with some hairs towards the base, paler green and with scattered hairs below with coarse hairs on the midrib and veins. *Inflorescences* axillary, subsessile to shortly pedunculate, 1- or 2-flowered; peduncles red, 2–3 mm long, hairy; bracts green, 9 × 5–6 mm, ovate, connate 4 mm from base, with some coarse hairs on midrib and margins, margin slightly serrate; bracteoles paired, green, 6–8 × 3 mm, oblong, with coarse hairs on midrib and margins; pedicels 2–3 mm long, glabrous. *Calyx* tubular, pale green, 10–11 mm long, upper lobes c.2 mm long, lower lobes c.3 mm long, acuminate, glabrous except for a few tufts of hair at apex. *Corolla* white with greenish yellow markings in throat, c.15 mm long overall, tube narrow in lower third, widening to mouth in apical two-thirds, hairy externally in the apical third, particularly densely so towards the mouth, upper lobes suborbicular, 3–4 × 3 mm, lower and lateral lobes suborbicular, 3 × 3 mm. *Stamens* 2; filaments c.5 mm long, attached c.6 mm from base of corolla, glabrous; anthers c.1 mm long, thecae parallel, coherent at apices; staminodes 2, c.0.5 mm long. *Gynoecium* c.10 mm long overall; disc

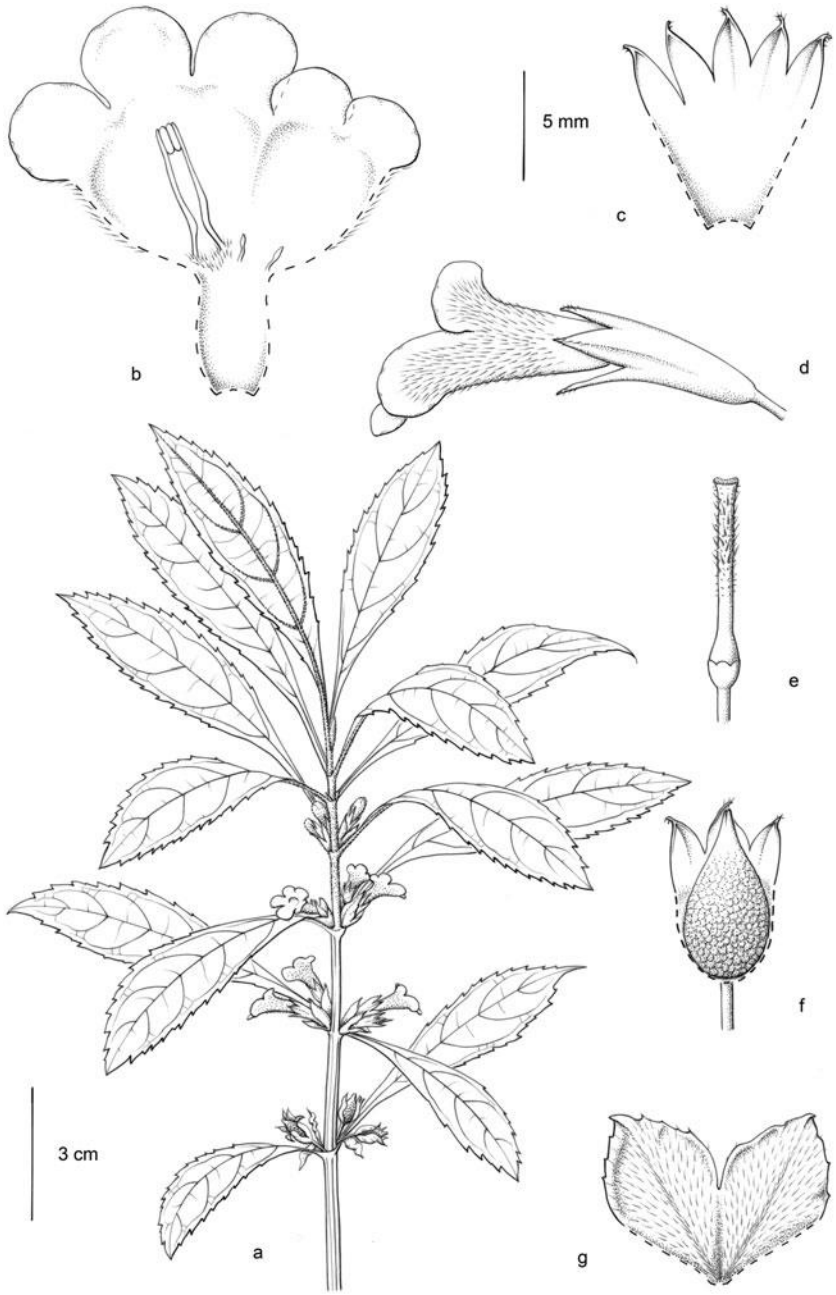


Fig. 6 . *Cyrtandra hekensis* Karton. & H.J.Atkins, sp. nov. A, Habit; B, corolla, longitudinal section; C, calyx, longitudinal section; D, flower, lateral view; E, gynoecium; F, fruit with persistent calyx partially removed; G, bracts. Drawn from *Hendrian* et al. 901 (E).

cupular with lobed margin, glabrous externally, c.1.5 mm long; ovary glabrous, style eglandular hairy towards apex; stigma slightly bilobed, lobes small, c.1 mm across. *Fruits* ovoid, glabrous, verrucose, drying light brown, 6 × 4 mm; base of style and calyx persistent, bracts sometimes persistent.

Distribution. Central Sulawesi: Luwuk (see Fig. 5).

Habitat and ecology. Lowland to lower montane forest from 420 to 660 m.

Etymology. Named after the mountain on which it was collected.

Proposed IUCN conservation category. As for *Cyrtandra albiflora* and *C. hendrianii*, this species is known only from Mount Hek, Luwuk Regency, where it was collected at relatively low altitude during expeditions in 2004 and 2008. This is an area with no formal protection (UNEP-WCMC & IUCN, 2016).

A lack of specimens precludes estimations of EOO and AOO, and it is not possible to comment on threats to this species with any certainty, but it is anticipated that the deforestation and clearing for agriculture reported for this habitat type (Cannon *et al.*, 2007) could threaten the only known populations of this species; we therefore recommend a category of Vulnerable (VU) using the criterion VUD2, because it is a population with a very restricted AOO or number of locations and, as such, is prone to the effects of human activities or stochastic events and is thus capable of becoming Critically Endangered or even Extinct in a short period of time, but emphasise the importance of carrying out further survey work in this region.

Additional specimen examined. **Central Sulawesi**: Luwuk, Mt Hek, 26 ii 2004, *Hendrian, Newman, M.F., Scott, S.M., Saleh, M.N. & Supriadi, D.* 901 (E).

This species can be distinguished from others on the island by a combination of its serrate, more or less isophyllous leaves, coarse indumentum, particularly on young growth, and white flowers with greenish yellow markings in the throat.

Cyrtandra hendrianii Karton. & H.J.Atkins **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its pink corolla and red calyx and long thin bracts and bracteoles. – Type: Indonesia, Central Sulawesi, Mt Hek, 660 m, 25 ii 2004, *Hendrian, Newman, M., Scott, S., Nazre Saleh & Supriadi, D.* 883 (holo BO, iso E). **Figs 5, 7**.

Shrub up to 2 m. *Stems* striate, reddish, more or less glabrous, slightly hairy in axils. *Leaves* opposite, subequal; petioles red, 2–4 cm long, densely hairy when young, becoming more glabrous with age, narrowly winged; blades, 16.4–29.5 × 5.7–9.5 cm, narrow oblong or elliptic to oblanceolate, apex acute to short acuminate, base attenuate, margin serrate; 8–11 pairs of lateral veins and with reticulate tertiary venation; dark green and mostly glabrous above with a few scattered hairs and on the tips of the marginal teeth, paler green below, with red to pink venation, densely fine hairy on midrib and veins with some scattered hairs on the blade. *Inflorescences* axillary, subsessile, with c.8–10 flowers at various stages of development; peduncle

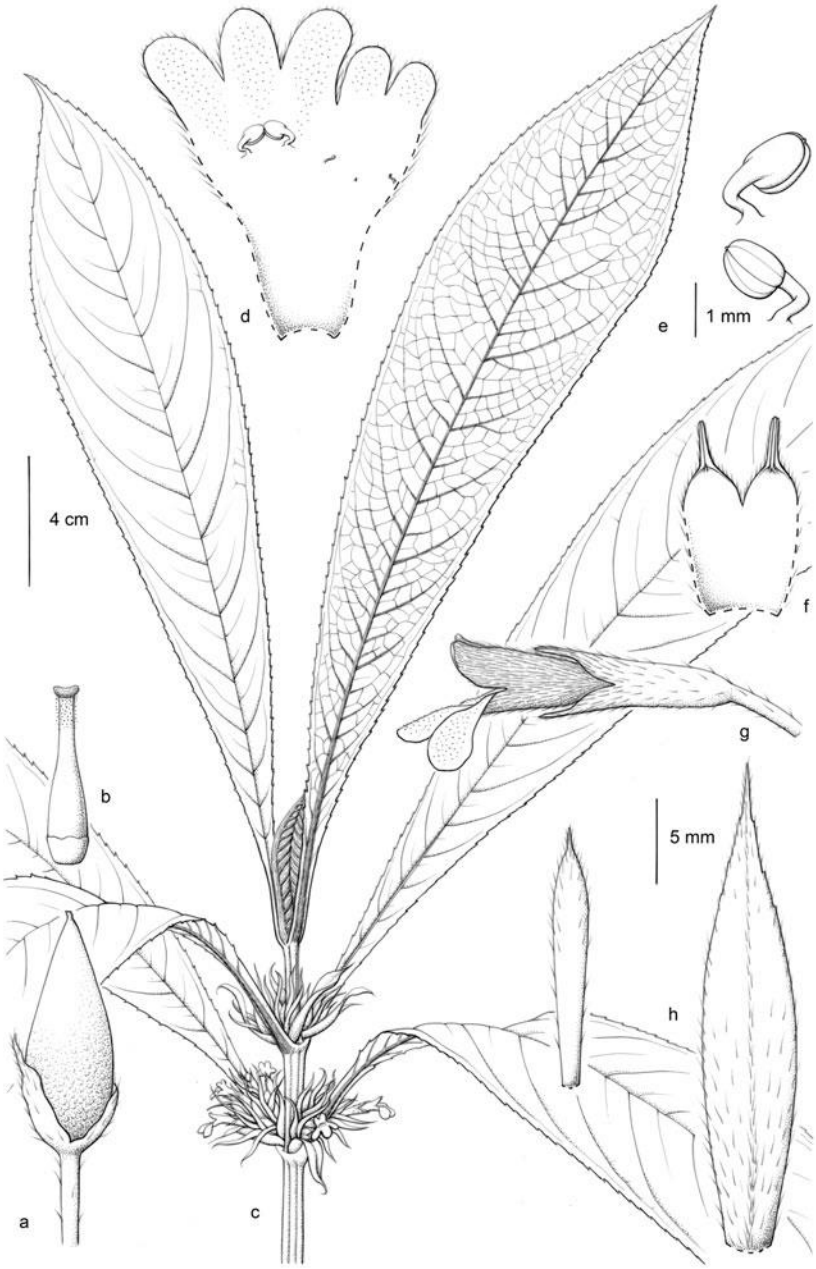


Fig. 7 . *Cyrtandra hendrianii* Karton. & H.J.Atkins, sp. nov. A, Fruit; B, gynoecium; C, habit; D, corolla, longitudinal section; E, anthers; F, calyx, longitudinal section; G, flower, lateral view; H, bract and bracteole. Habit and fruit drawn from *Hendrian* et al. 883 (E). All other parts drawn from *Scott* 503 (E) (accession 20040646A).

1–2 mm, sparsely hairy; bracts greenish, 25–35 × 5–6 mm, oblong to lanceolate, acuminate, with shallowly serrate margins and a few scattered hairs externally, more densely hairy along the margins and at the apex; bracteoles 15–20 mm long, lanceolate to linear, long acuminate, sparsely hairy, more densely hairy along margins and particularly at the apex; pedicels 5–7 mm long sparsely hairy, extending slightly in fruit. *Calyx* tubular, red, 7–8.5(–10) mm long, appearing bilobed, lobes triangular, 3–3.5(–5) mm long, acuminate, divided very briefly at the apex into three in the upper lobe and two in the lower, sparsely hairy at the base, more densely so at apex. *Corolla* pink, 15–18 mm long, narrow funnel form, lobes suborbicular, lower lobes slightly more elongate, spreading to somewhat recurved, c.4 × 3 mm, hairy externally with a dense covering of short glandular hairs on the inside of lobes and in the mouth of the corolla. *Stamens* 2; filaments short, 1.5–2 mm long, attached c.8 mm from base of corolla, glabrous; anthers c.1 mm long, glabrous, cohering at apices; staminodes 3, c.1 mm long. *Gynoecium* 10 mm long; disc cupular, 2 mm long, glabrous with undulating margin; ovary glabrous; style with short, glandular hairs particularly towards the apex; stigma bilobed, c.1 mm across. *Fruits* ovoid to ellipsoid or rather elongate, glabrous, somewhat verrucose, drying dark brown, 11–15 × 4–7 mm; base of style and calyx persistent.

Distribution. Central Sulawesi (see Fig. 5).

Habitat and ecology. Lower montane forest from 660 to 680 m.

Etymology. Named after Hendrian, director of Purwodadi Botanic Garden, Java, and also one of the collectors of this new species.

Proposed IUCN conservation category. This species is known from two collections made on the same trip to Mount Hek in 2004 at mid-altitude (660–680 m). As stated for *Cyrtandra albiflora*, this area does not currently receive any formal protection (UNEP-WCMC & IUCN, 2016). The low number of collections precludes calculations of EOO and AOO. Given the threat of deforestation in lower montane forest habitat on the island (Cannon *et al.*, 2007; Thomas *et al.*, 2011), we recommend a category of Vulnerable (VU) using the criterion VUD2, because it is a population with a very restricted AOO or number of locations, but emphasise the importance of carrying out further survey work in this region.

Additional specimen examined. **Central Sulawesi**: Luwuk, Mt Hek, Sungai Spa, 25 ii 2004, *Scott, S.* 04–316, grown at RBGE as accession 20040646A, vouchered as *Scott* 503 (E).

This species is most similar to *Cyrtandra albiflora* (described here and collected from the same location). It can be distinguished, however, by significant differences in corolla and calyx colour, density of indumentum on the stems and leaves and the size and shape of the bracts and bracteoles, which are explained in more detail under that species.

Cyrtandra hispidula Karton. & H.J.Atkins **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its coarse, white, hispid indumentum, broad leaves and large, leaf-like inflorescence bracts. – Type:

Indonesia, South Sulawesi, Mt Rantemario, 2527 m, 25 iv 2009, *Thomas, D.C. & Ardi, W.H.* 09–86 (holo BO; iso E, L). **Figs 5, 8**.

Coarse herb to 150 cm. *Stems* ridged, striate, green, densely hairy on young growth and around axils, hairs coarse, pale, 1–3.5 mm long. *Leaves* opposite, subequal, drying dark brown; petioles green, 2.5–5.5 cm long, densely hairy; blades 14–16 × 9–10 cm, broad elliptic to ovate, apex acuminate, base cuneate, slightly asymmetrical, margin serrate; 8 or 9 pairs of lateral veins and reticulate tertiary venation, dark glossy green, slightly marbled with scattered, long multicellular hairs above, covered with dense, multicellular hairs on midrib and veins below. *Inflorescences* axillary, subsessile, 1- or 2-flowered; peduncle up to 5 mm long, densely hairy; bracts green, 25–40 × 8– 20 mm, paired, leaf-like, broad elliptic to ovate, with a covering of dense, coarse white hairs, especially on veins, margins serrate, apex acute; pedicels green, 13–15 mm long, hairy, continuing to elongate up to 40 mm with the developing fruit. *Calyx* tubular, green, c.25 mm long, lobes acuminate, lower lobes c.10 mm long, upper lobes c.8 mm long, hairy, densely so at the base with a distinctive fringe of hairs. *Corolla* white, turning brown with time, tube completely enclosed within calyx, only lobes visible, c.18 mm long overall, tube glabrous externally and with a scattering of small glands in the mouth of the corolla, all lobes rounded, lateral lobes with shallowly serrate margins, upper lobes 5–6 × 4 mm, lower and lateral lobes c.8 × 5 mm. *Stamens* 2; filaments c.3 mm long, attached c.8 mm above the base of the corolla, straight, almost glabrous, with a few scattered, glandular hairs; anthers c.3 mm long, thecae parallel, with stalked glandular hairs on the back, not coherent; staminodes 3, c.2 mm long. *Gynoecium* c.12 mm overall; disc cupular with undulating margin, c.2 mm long, glabrous; ovary glabrous; style with some glandular hairs, particularly towards the apex; stigma bilobed, c.1 mm across. *Fruits* elongate, glabrous, smooth, green, drying dark brown, 18–25 × 5–8 mm; calyx and base of style persistent.

Distribution. South Sulawesi: Latimojong Range (see Fig. 5).

Habitat and ecology. Montane forest associated with *Rhododendron*, *Vaccinium* and *Leptospermum* at c.2500 m altitude.

Etymology. Named after its distinctive hispid indumentum on most parts of the plant.

Proposed IUCN conservation category. It has not been possible to calculate EOO and AOO for this species, owing to the low number of collections. This species has been collected only twice, and the locality is not within a protected area (UNEP-WCMC & IUCN, 2016). It is, however, found in montane forest, which is one of the least threatened forest types in Sulawesi (70% of upland forests above 1500 m elevation are intact). Montane and tropical alpine forests are not considered to be endangered, with a substantial majority of these sites across the island still in good condition (Cannon *et al.*, 2007). We suggest the category of Least Concern (LC) for this species.

Additional specimen examined. **South Sulawesi**: Mt Batutoding, 1913, *Rachmat* 916 (BO).

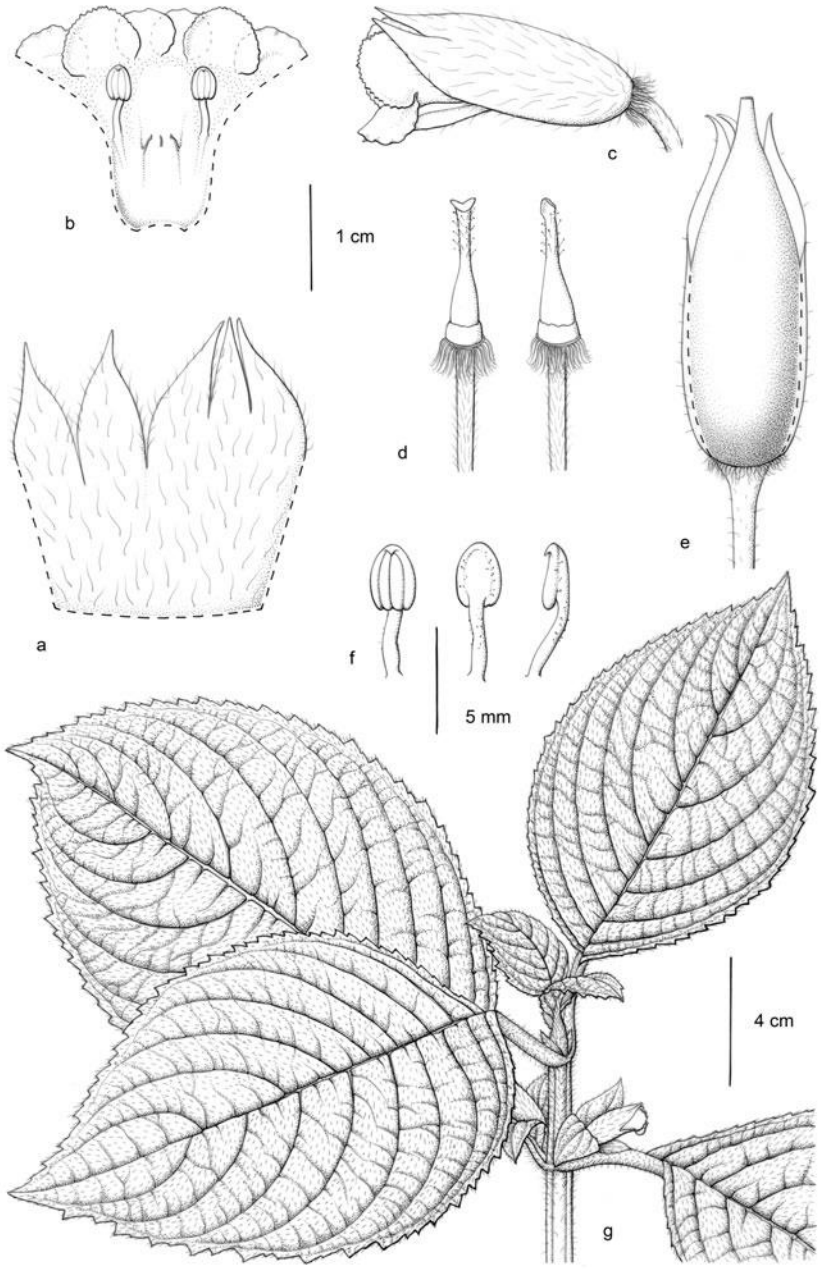
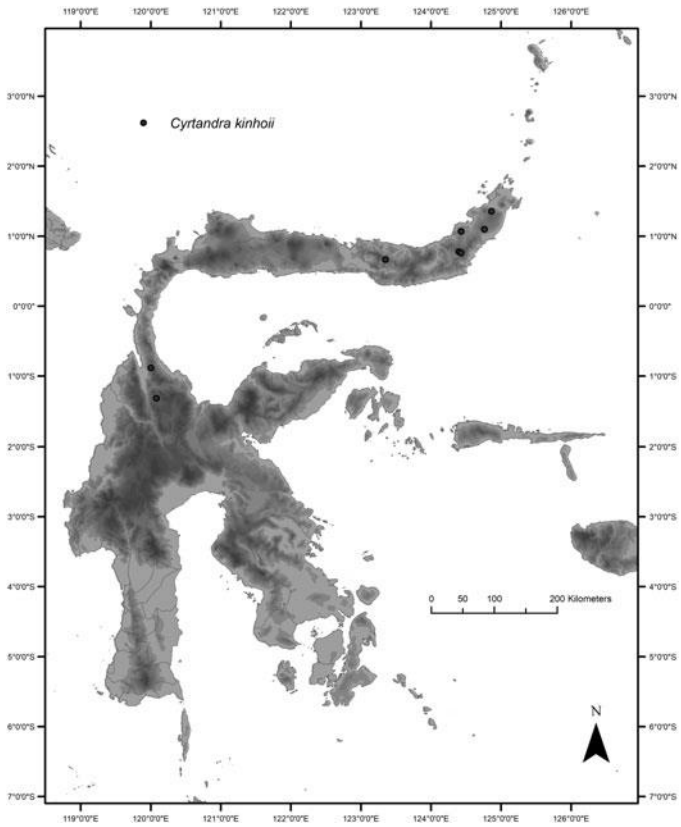


Fig. 8 . *Cyrtandra hispidula* Karton. & H.J.Atkins, sp. nov. A, Calyx, longitudinal section; B, corolla, longitudinal section; C, flower, lateral view; D, gynoecium; E, fruit with persistent calyx partially removed; F, anthers; G, habit. Drawn from *Thomas & Ardi* 09–86 (E).



Fi g. 9 . Known distribution of *Cyrtandra kinhoii* Karton. & H.J.Atkins.

This description is based primarily on material from the type, *Thomas & Ardi* 09–86, but *Rachmat* 916 appears to be the same taxon with the same distinctive indumentum and inflorescence bracts, although it is overall a much smaller plant. The description of the flowers is based on a single, slightly immature flower. The combination of the coarse, hispid, white indumentum, broad leaves and large, leaf-like inflorescence bracts distinguishes it from any other *Cyrtandra* species on the island.

Cyrtandra kinhoii Karton. & H.J.Atkins **sp. nov.**

This species shares tessellate stems and decurrent, subequal leaves with *Cyrtandra fasciata* H.J.Atkins. It can be distinguished, however, by its longer leaf blades (30–60 cm versus 14–22 cm), bract shape and length (oblong-lanceolate bracts, 30–45 20–25 mm, versus linear bracts, 20 2 mm) and corolla colour (corolla white × flushed slightly pink with no markings versus corolla yellow with red stripes on lobes). – Type: Indonesia, North Sulawesi, Mt Ambang Nature Reserve, Paya Paya, near Sinsingon village, 1252 m, 2 xi 2016, *Barber, S., Atkins, H., Kartonegoro, A. & Kinho, J.* BAKK 36 (holo BO; iso E, L). **Figs 9, 10**.

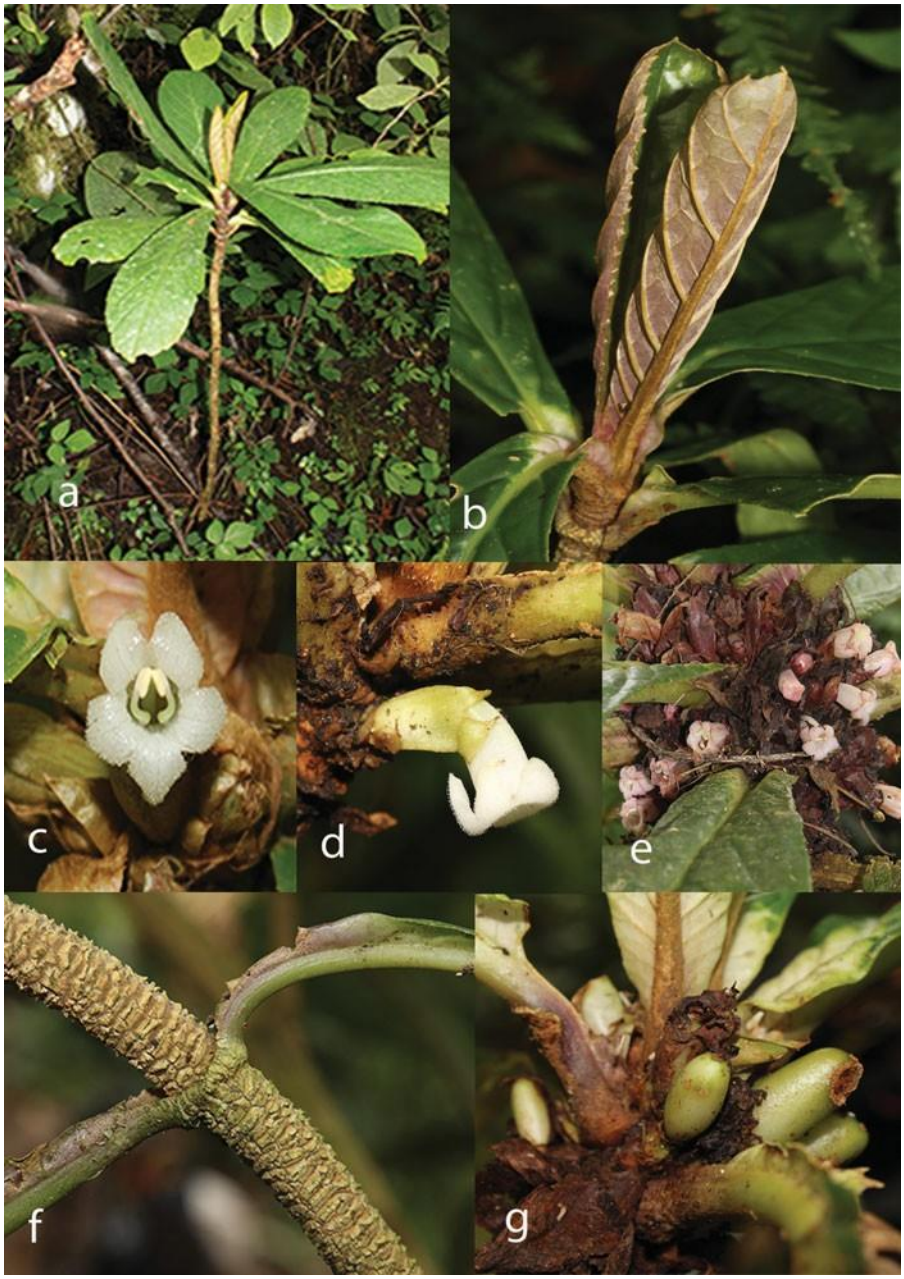


Fig. 10. *Cyrtandra kinhoii* Karton. & H.J.Atkins, sp. nov. A, Habit; B, young leaves; C, corolla, anterior view; D, corolla, lateral view; E, inflorescence; F, tessellate stem; G, young fruits. (Photographs by Sadie Barber.)

Shrub 1–3 m or small tree 6–7 m. *Stems* tessellate, glabrous, sparsely hairy on younger growth, woody. *Leaves* opposite; subequal to somewhat unequal; petioles 1.5–2 cm long, winged; blades 30–60 × 10–15 cm, elliptic to obovate to oblanceolate, usually crowded at the ends of branches, apex short acuminate, rarely obtuse, base attenuate, margin serrate; 10–20 pairs of lateral veins and reticulate tertiary venation, curving upwards and running out to the margin, occasionally branching near the margin, glabrous, mid-green above, sparsely hairy and paler green below, more densely hairy on midrib and veins and occasionally flushed red at base of leaf. *Inflorescences* axillary, subsessile, congested, with up to c.15 flowers at various stages of development; bracts oblong-lanceolate, light green, flushed slightly reddish, leathery, 3–4.5 × 2–2.5 cm, subglabrous to sparsely hairy, slightly warty, apex acute or short acuminate, caducous; bracteoles lanceolate, light green, subglabrous c.3 × 1 cm, leathery, apex acuminate; pedicels 4–7 mm long, light green, glabrous to sparsely hairy. *Calyx* tubular, 21–25 mm long, light green to dark reddish brown, sparsely hairy, warty at base, lobes acuminate, lower lobes divided c.12 mm from apex, upper lobes less deeply divided, 8–10 mm from apex, densely hairy. *Corolla* white or flushed slightly pink, 35 mm, narrow in basal third to half, gradually widening to mouth, glandular hairy externally, densely so internally, lobes strongly recurved, upper lobes suborbicular, 6 × 5 mm, lower and lateral lobes suborbicular to slightly oblong, 5–10 × 5–7 mm, lobes with dense covering of glandular hairs. *Stamens* 2; filaments 2–8 mm, attached 12–20 mm above the base of corolla, glabrous, light green; anthers 2–3 mm, thecae slightly divaricate, coherent at apices, cream; staminodes 3, lateral c.1.5 mm long, central c.0.5 mm long. *Gynoecium* 25–30 mm overall; disc cupular with undulate margin, lower on one side, glabrous, 2–3 mm; ovary glabrous; style white, glabrous, densely eglandular hairy at apex (or densely eglandular hairy for whole length in Central Sulawesi specimens); stigma light green, bilobed, lobes 3–4 × 2–3 mm, vertical or spreading, densely glandular hairy on inner surface of lobes. *Fruits* ovoid to ellipsoid, glabrous, 10–15 × 5–8 mm, green when unripe; bracts and calyx not persistent, base of style occasionally persistent.

Distribution. North Sulawesi and Central Sulawesi (see Fig. 9).

Habitat and ecology. Lower montane to submontane forest at 700–1300 m.

Etymology. Named after Julianus Kinho, researcher at the Forestry Research Institute of Manado, North Sulawesi, and one of the collectors of the type specimen.

Proposed IUCN conservation category. This is a relatively widespread species on Sulawesi, collected so far from three of the island's provinces. The proposed conservation category based on the EOO calculated using GeoCAT is Near Threatened (NT), and the category based on the estimated AOO is Endangered (EN). Most of the collections, however, fall within the boundaries of Bogani Nani Wartabone National Park in Gorontalo, Lore Lindu National Park in Central Sulawesi or Mount Ambang Nature Reserve in North Sulawesi, where threats from deforestation should be somewhat reduced. We therefore consider this species to be of Least Concern (LC) at present.

Additional specimens examined. **North Sulawesi**: Minahasa Regency, Mt Masarang, 10 i 1895, *Koorders* 17187β (L); Lolombulan, 6 iv 1895, *Koorders* 17191β (BO, L); G. Manimporok, Soputan Mts, 18 vi 1954, *Alston* 15926 (BM); Tomohon, Mt Mahawu, 23 vi 1956, *Forman* 223 (K, L); East Bolaang Mongondow, Mt Ambang, 3 xi 2016, *Barber* et al. BAKK 65 (BO, E). **Gorontalo**: Mt Gambuta, 10 iv 2002, *Atkins* et al. 56 (BO, E). **Central Sulawesi**: Between Palu and Parigi, 17 Apr 1975, *Meijer* 9364 (BO, L); Road to Lake Lindu, c.60 km SSE of Palu, 30 v 1979, *van Balgooy* 3565 (A, BO, E, L); Road to Lake Lindu, c.60 km SSE of Palu, 30 v 1979, *van Balgooy* 3571 (A, BO, E, L).

Most of the detail of this description has been written using recent collections from Gorontalo and North Sulawesi. The material of the three collections from Central Sulawesi is much poorer, but they are strikingly similar vegetatively and the few flowers available for dissection were a close match, with the exception of style indumentum (noted in the description). These specimens are included here, although further collections may provide evidence for the recognition of two distinct species in the future.

This species is most similar to *Cyrtandra fasciata* from Central Sulawesi, in that these species both have tessellate stems and decurrent leaves, but it can be distinguished by its leaf blades 30–60 cm (versus leaf blades 14–22 cm); bract shape and length (oblong-lanceolate bracts, 30–45 × 20–25 mm versus linear bracts, 20 × 2 mm) and corolla colour (corolla white or flushed slightly pink without markings versus corolla yellow with red stripes on lobes).

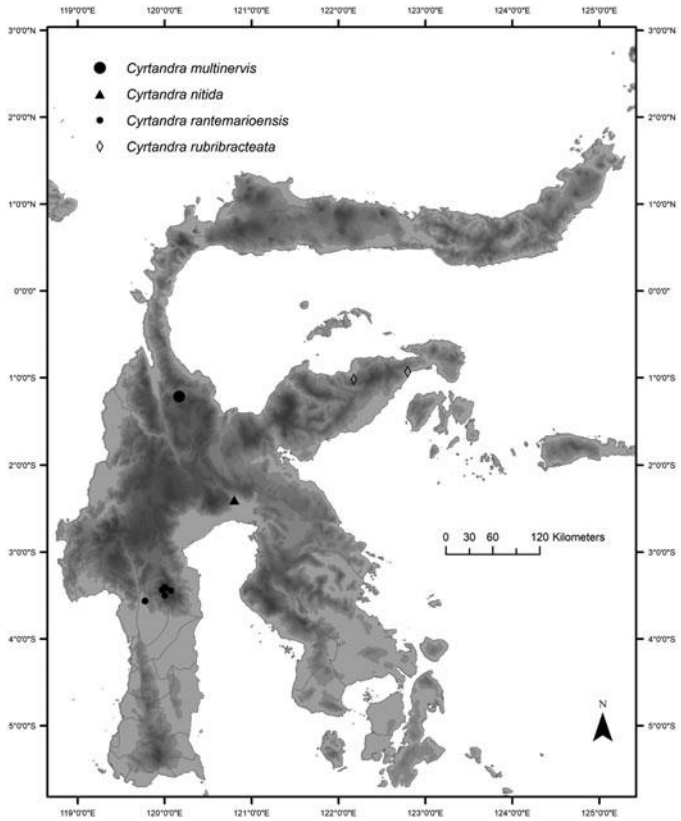
One of the collections included here (*Koorders* 17187β) has been annotated with the name *Cyrtandra similis* Koorders. This appears to be a manuscript name used by Koorders but never published. The name *Cyrtandra similis* is used later for an unrelated Philippine species by Quisumbing (Quisumbing, 1930).

The young leaves of this plant are reported to be collected and used as a vegetable known as *soroako*.

Cyrtandra multinervis Karton. & R.Bone **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its high number of lateral veins, and narrow fruits. – Type: Indonesia, Central Sulawesi, Tongoa, Mt Potong, 980 m, 8 iii 2001, *Kessler, P.J.A.* et al. PK 2974 (holo BO; iso E, K, L). **Figs 11, 12**.

Branching shrub up to 4 m. *Stems* ridged, striate, glabrous. *Leaves* opposite, subequal; petioles 4–5 cm long, glabrous; blades up to 31 × 9.5 cm, oblong or narrow elliptic, apex acuminate, base attenuate, somewhat oblique, margin subentire to minutely and distantly crenulate; 17–19 pairs of lateral veins and faint, reticulate tertiary venation, dark green and glabrous above, paler green and glabrous below. *Inflorescences* axillary, 1- to 5-flowered; peduncle 15–18 mm long, glabrous; bracts 20–23 × 9–12 mm, enclosing the flowers when in bud, ovate, glabrous; bracteoles, 9–11 × 3–4 mm, ovate-elliptic, glabrous; pedicels 6–8 mm long, glabrous. *Calyx* tubular, pale green, 16–18 mm long, glabrous, lower lobes acuminate, 7–8 mm long, upper lobes, 3–4 mm long. *Corolla* white with red in the throat, 18–23 mm long, glabrous, lobes recurved, just showing



Fi g. 1 1 . Known distribution of *Cyrtandra multinervis* Karton. & R.Bone, *Cyrtandra nitida* Karton. & H.J.Atkins, *Cyrtandra rantemarioensis* Karton. & R.Bone and *Cyrtandra rubribracteata* Karton. & H.J.Atkins.

above the top of the calyx, upper lobes suborbicular, c.6 × 4 mm, lower and lateral lobes suborbicular, c.4 × 3 mm. *Stamens* 2; filaments 5–7 mm long, attached c.9–10 mm above the base of the corolla, glabrous; anthers c.2 mm, thecae parallel, cohering at apices. *Gynoecium* c.15 mm overall; disc cupular c.1 mm long, glabrous; ovary glabrous; style glabrous at base, short hairy at apex; stigma bilobed, c.1 mm across. *Fruits* cylindrical, narrow, sometimes curved, drying black, (10–)17–25 × 1–2 mm, glabrous, smooth; base of style persistent, calyx not persistent.

Distribution. Central Sulawesi, known only from the type locality in Tongoa (see Fig. 11).

Habitat and ecology. Lower montane forest at c.980 m.

Etymology. Named for the high number of lateral veins on the leaf blades.

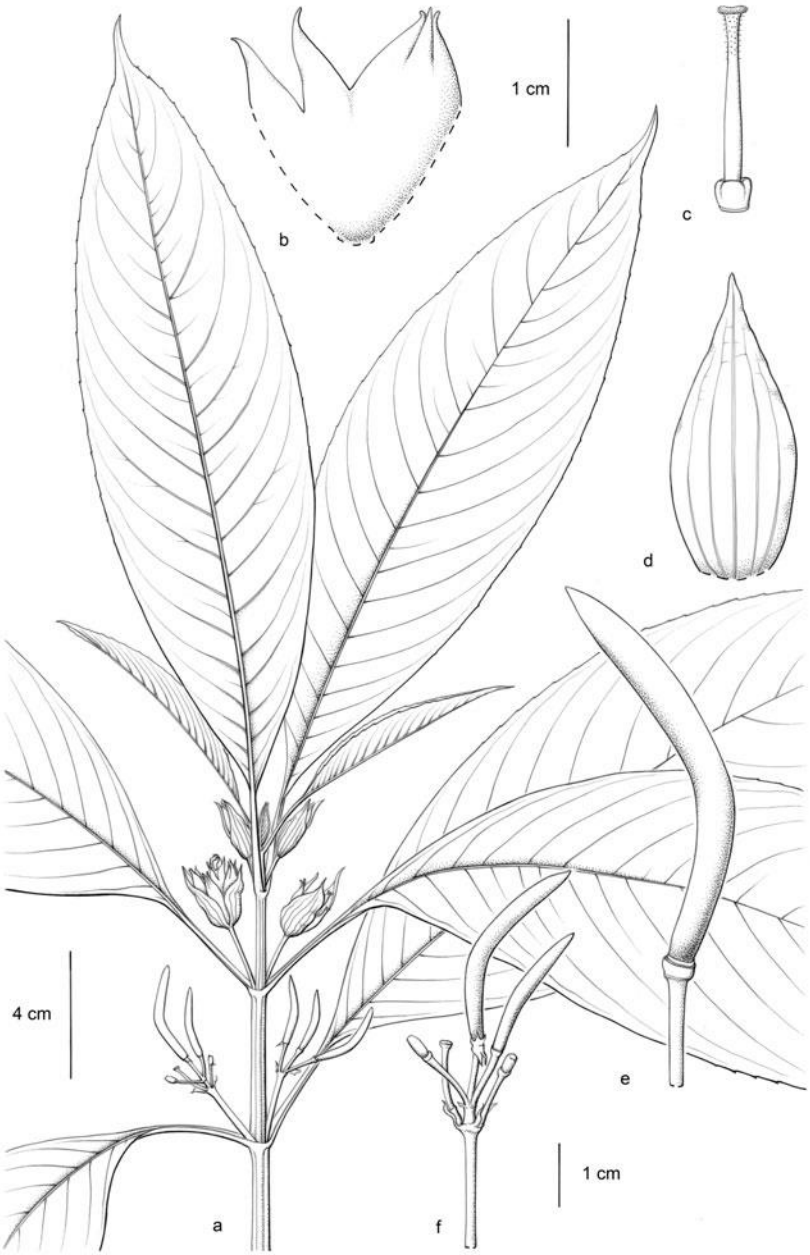


Fig. 12. *Cyrtandra multinervis* Karton. & R.Bone, sp. nov. A, Habit; B, calyx, longitudinal section; C, gynoecium; D, bract; E, fruit; F, infructescence. Drawn from *Kessler* et al. PK 2974 (E, K, L).

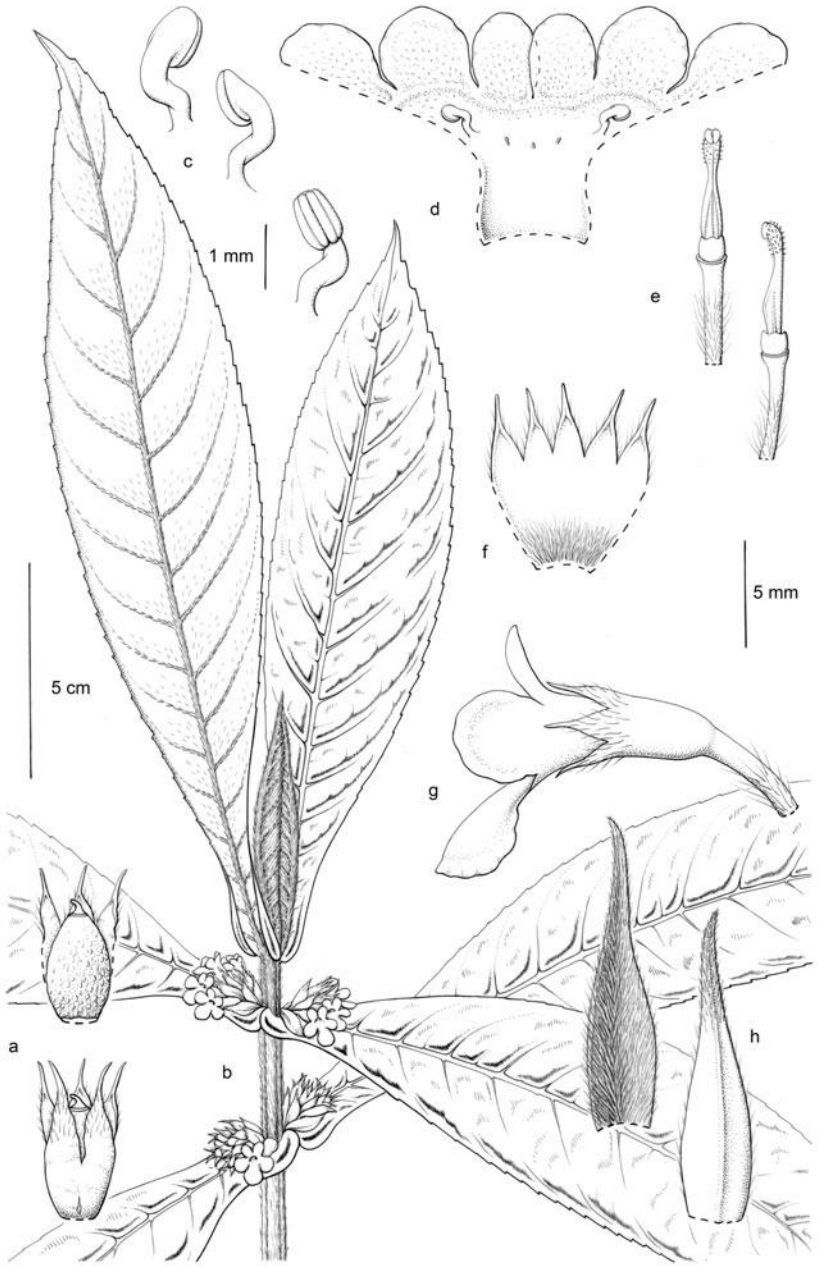
Proposed IUCN conservation category. It has not been possible to calculate EOO and AOO for this species, because it is known only from the type collection. This collection falls within the limits of the Lore Lindu National Park (a Unesco Biosphere Reserve) and, as such, will have some protection (Schwarze *et al*., 2009). It has been collected only once from a relatively well collected area of Sulawesi, suggesting it is probably not locally abundant. We suggest a category of Vulnerable (VU) for this species, using the criterion VUD2, because it is a population with a very restricted AOO or number of locations, but emphasise the importance of carrying out further survey work in this region.

This species has been described from a single collection but is very distinctive owing to its narrow fruits and many-nerved leaves.

Cyrtandra nitida Karton. & H.J.Atkins **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its glossy leaves, strongly auriculate leaf bases and clusters of white flowers. – Type: Indonesia, Central Sulawesi, North of Mangkutana, Wotu–Lake Poso road, c.1150 m, 20 ii 2000, *Mendum, Argent & Hendrian* 00111 (holo BO, iso E). **Figs 11, 13**.

Herb up to 2 m in height, sometimes branching from the base. *Stems* longitudinally ridged, flushed purple, sparsely woolly-hairy, more densely so on young growth. *Leaves* opposite, unequal, both well developed; blades 15.5–30.5 × 4.5–9 cm, oblong to narrowly oblong, apex acuminate, base attenuate becoming auriculate, clasping the stem and touching the base of the opposite leaf, margin serrulate; 11–15 pairs of lateral veins, tertiary venation obscure; dark glossy green turning almost white at the base, more or less glabrous with some scattered hairs above; much paler below with a sparse covering of fine, golden hairs, more densely so on the midrib and veins. *Inflorescences* axillary, tucked into the auriculate leaf bases, with c.10–12 flowers at various stages of development; single bract green, 15–22 × 5–8 mm, lanceolate-ovate, apex acuminate, margin slightly serrate, densely hairy above, less so below, caducous; bracteoles lanceolate, green, 15–20 × 4–5 mm; pedicels light green, 3–5 mm long, hairy. *Calyx* green, 7–8 mm long, more or less evenly 5-lobed, lobes divided almost halfway to the base, 3–4 mm, acuminate, sparsely hairy, more densely so on lobes. *Corolla* white, 8–12 mm long, tube narrow, lobes spreading, slightly projecting forwards, upper and lateral lobes orbicular, c.5 × 4 mm, lower lobe slightly longer and ovate, c.6 × 4 mm, subglabrous externally, with a dense covering of short, glandular hairs on the inside of the lobes and the mouth of the tube. *Stamens* 2; filaments 1–2 mm long, attached c.4 mm from the base of the corolla, glabrous; anthers 1 mm long, thecae parallel, glabrous; staminodes 3, c.0.5 mm long. *Gynoecium* 4–6 mm overall; disc cupular with undulating margin, c.1 mm long, glabrous; ovary glabrous at base; style glandular hairy towards apex; stigma bilobed, lobes vertical on specimens seen, 0.8–1 mm across. *Fruits* ovoid, dark green, brown and verrucose when dry, 4–5 × 2–3 mm; most of calyx and base of style persistent.



Fi g. 13. *Cyrtandra nitida* Karton. & H.J.Atkins, sp. nov. A, Fruit with and without persistent calyx; B, habit; C, anthers; D, corolla, longitudinal section; E, gynoecium; F, calyx, longitudinal section; G, flower, lateral view; H, bracts. Habit and fruit drawn from *Sidiyasa* 1369 (K, L). Flowers drawn from *Mendum* et al. 00111 (E).

Distribution. Central and South Sulawesi, close to the border of both provinces (see Fig. 11).

Habitat and ecology. Steep, rocky roadside banks on edge of primary forest at 500–1150 m.

Etymology. Named for its distinctive glossy leaves.

Proposed IUCN conservation category. It has not been possible to calculate EOO and AOO for this species, owing to the low number of collections. Both collections were described as being in disturbed roadside vegetation and at relatively low altitude. It has not been possible to accurately georeference either collection, but it is possible that they were made within the limits of the Pegunungan Faruhumpenai Nature Reserve. We recommend that this species be recognised as Vulnerable (VU) using the criterion VUD2, because it is a population with a very restricted are of occupancy or number of locations, and emphasise the importance of carrying out further survey work in this region.

Additional specimen examined. **South Sulawesi**: 21 km south of border line between S. Sulawesi and C. Sulawesi, 12 xii 1994, *Sidiyasa* 1369 (K, L).

This species is very distinctive and unlike any others in Sulawesi owing to its glossy upper leaf surface and the auriculate leaf bases which clasp the stem and hold the inflorescence.

Cyrtandra rantemarioensis Karton. & R.Bone **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its long, trailing inflorescence stems, bright red, arcuate corollas and elongate fruits. – Type: Indonesia, South Sulawesi, Mt Rantemario, 1750 m, 5 iii 2000, *Mendum* et al. 00240 (holo BO; iso E, L). **Figs 11, 14**.

Branching subshrub up to 2 m, often much shorter. *Stems* striate, greenish brown, glabrate, sparsely hairy on young growth. *Leaves* opposite, sometimes clustered at the ends of the stems, more or less equal; petioles 1.5–2 cm long, sparsely hairy; blades 8–20 × 1.8–5 cm, oblong to narrowly obovate, apex short acuminate, base attenuate, margin serrate; 5 or 6 pairs of lateral veins, tertiary venation loosely reticulate, mid- to dark green, somewhat marbled and subglabrous to sparsely hairy above, much paler and flushed purple and subglabrous below, very sparsely hairy on midrib and veins. *Inflorescences* borne on trailing stems from the base of the plant, subsessile, 1- or 2-flowered, inflorescence stem striate, hairy when young, becoming glabrous with age, c.1 mm in diameter with persistent bracteoles; bracts green to dull red, c.25 × 10 mm, somewhat lanceolate, acuminate at apex, with serrate margins apically, hairy when young, particularly at the base and along veins, soon caducous, visible only at the tips of the inflorescence stems; bracteoles green to dull red, 10–15 × 2 mm, linear to linear-lanceolate, acuminate at apex, sparsely hairy externally, often persistent on inflorescence stem; pedicels reddish, 10–15 mm long, hairy, elongating

Fig. 14. *Cyrtandra rantemarioensis* Karton. & R.Bone, sp. nov. A, Habit; B, trailing inflorescence; C, corolla, anterior view; D, young fruits; E, flower, lateral view. (Photographs: A–D, Axel Poulsen; E, Steve Scott.)

and becoming more glabrous in fruit. *Calyx* reddish when in flower turning olive green when fruiting c.6 mm long, upper lobes divided briefly at apex, lower lobes free to base, lobes acuminate, sparsely hairy externally. *Corolla* red, slightly paler in the mouth, 15–20 mm long, arcuate with a narrow tube widening to mouth, sparsely hairy externally, internally with scattered eglandular hairs and a dense covering of glandular hairs in the mouth, lobes spreading, slightly projected forwards, two upper lobes orbicular, c.7 × 7 mm, lateral and lower lobes orbicular, 9–10 × 8 mm. *Stamens* 2; filaments c.2 mm, attached c.12 mm above the base of the corolla, white, glabrous; anthers 1– 2 mm long, cohering at apices, thecae parallel, glabrous, white; staminodes 3, c.0.5 mm long. *Gynoecium* c.10 mm long overall; disc 2 mm long, unilateral with undulating to lobed margin, glabrous; ovary densely hairy; style glandular hairy towards apex; stigma bilobed, lobes vertical on specimens seen, c.1 mm across. *Fruits* elongate, glabrous, smooth, greenish brown (drying light brown), 15–30 × 4–8 mm; base of style and calyx persistent.

Distribution. South Sulawesi: Latimojong Range (see Fig. 11).

Habitat and ecology. Montane forest at 1500–2600 m.

Etymology. Named after the mountain where it was collected.

Proposed IUCN conservation category. Based solely on the EOO and AOO, this species would be in the Endangered (EN) category (based on a 2 ×2 km grid cell size) under the B criteria. It has, however, been collected on eight different botanical expeditions in the Latimojong Range (between 1969 and 2010), suggesting it is locally abundant and is found in montane forest *sensu* Cannon *et al.* (2007), which is one of the least threatened forest types in Sulawesi (70% of upland forests above 1500 m elevation are intact). For this reason, we recommend that this species be recognised as Least Concern (LC).

Additional specimens examined. **South Sulawesi**: Rantemario, Buntu Kaciling, 11 vi 2010, *Kartonegoro, A. & Santoso, W.* ARK475 (BO); Latimojong Mts, on path to Mt Rantemario peak, 6 vii 2002, *Brown, G., Craven, L.A. & Juswara, L.S.* 4 (BO); Latimojong Mts, Enrekang District, 28 i 2009, *Ardiyani, M., Poulsen, A.D. & Firdaus* 165 (E); Enrekang, Rantemario, 23 iv 2009, *Thomas, D. & Ardi, W.H.* 09–79 (E); Rantelemo, v 1929, *Kjellberg, G.K.* 4040 (BO); Latimojong Mts, Enrekang District, 30 x 1969, *Sands, M.J.S.* 307 (K); Enrekang, Rantemario, iii 2000, *Mendum, M., Argent, G.C.G. & Hendrian* 00240 (E); Mt Rantemario, 5 iii 2000, *Smith, P. & Galloway, L.* 229, grown at RBGE as accession 20000622K, vouchered as *Scott* 507 (E); Enrekang, 15 vi 1937, *Eyma, P.J.* 467 (BO, L).

There are four species in Sulawesi that share the phenomenon of flowering on long, trailing inflorescence stems that originate at the base of the plant. The other species in this group are *Cyrtandra geocarpa* Koord., *Cyrtandra hypogaea* Koord. and *Cyrtandra luteiflora* H.J.Atkins. This species can most easily be distinguished from the others in this group by its red flowers and elongate fruits, which although wrinkled when dry, are not as distinctly tessellate as the fruits of *Cyrtandra hypogaea*. It also appears

to be restricted to the mountains of the Latimojong Range, specifically to Mount Rantemario.

Cyrtandra rubribracteata Karton. & H.J.Atkins **sp. nov.**

Distinguished from other species in Sulawesi by a combination of its faded red bracts, pink calyx, narrow serrate leaves and beaked anthers. – Type: Indonesia, Central Sulawesi, Luwuk Regency, Mt Hek, 980 m, 28 ii 2004, *Hendrian, Newman, M., Scott, S., Saleh, N. & Supriadi, D.* 968 (holo BO, iso E). **Figs 11, 15**.

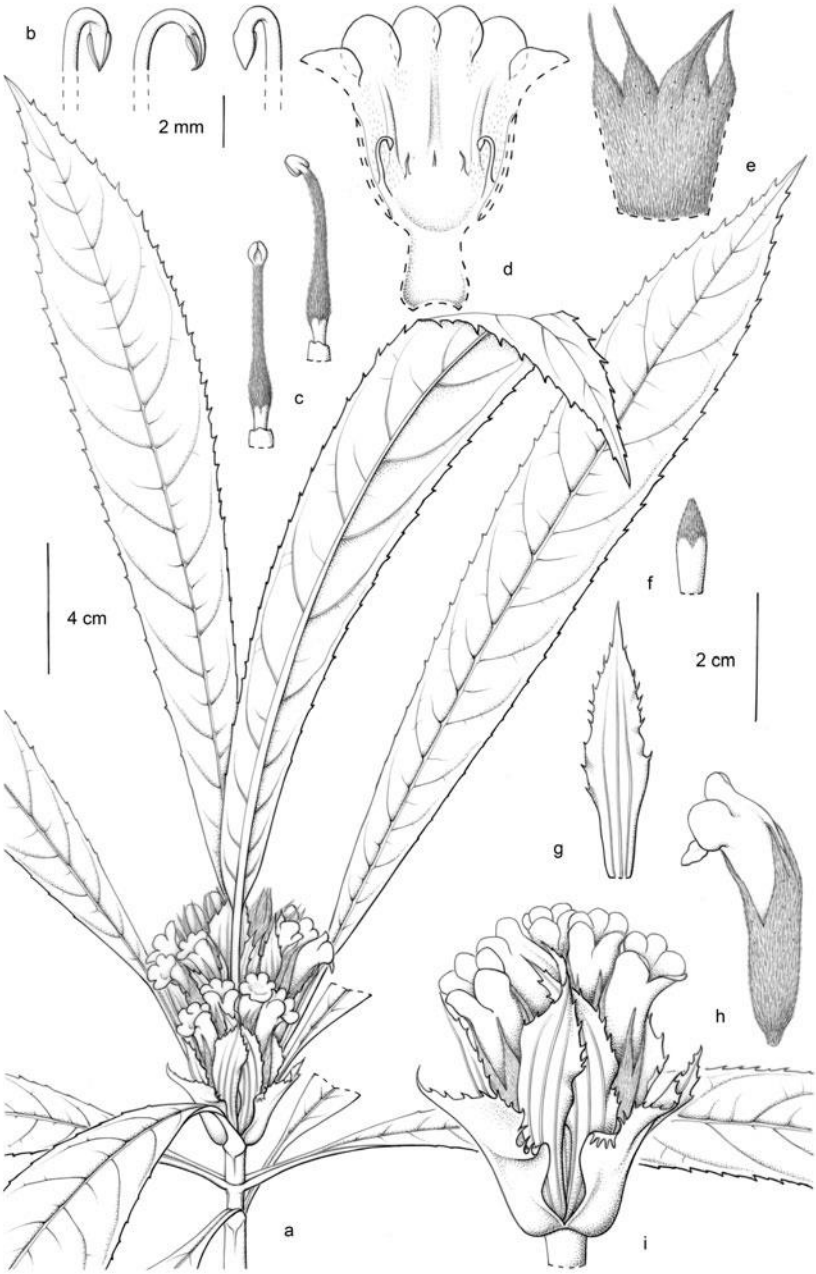
Shrub or treelet up to 1.8 m. *Stems* cylindrical, striate, glabrous. *Leaves* opposite, subequal; petioles 1.5–2 cm, glabrous; blades 14–25 × 2–3.5 cm, narrowly oblong to lanceolate, apex acuminate, base attenuate, margin serrate, occasionally biserrate; 5–7 pairs of lateral veins curving sharply upwards and faint tertiary venation, dark green and glabrous above, whitish green and glabrous below. *Inflorescences* axillary, sessile, c.6-flowered; bracts ovate, paired, dark, dull red, 3 × 2 cm, tough, leathery, joined very briefly at the base and forming an involucre with serrate margins, glabrous externally, enclosing the flowers and fruit; bracteoles c.4 × 1 cm, some much smaller, narrow lanceolate with serrate margins, leathery, glabrous; pedicels 4–6 mm long, hairy. *Calyx* tubular, pink, 30–36 mm long overall, lobes 9–17 mm long, acuminate, ridged along the length of the tips, hairy externally. *Corolla* white, 42–45 mm long overall, held upright in involucre, narrow in basal third, widening to mouth in upper two-thirds, upper lobes rounded, 5–6 × 4–5 mm, lower and lateral lobes suborbicular 8–9 × 7–8 mm, distinctive ridges running along base of the tube, densely hairy externally. *Stamens* 2; filaments c.10 mm long, attached c.20 mm above the base of the corolla, straight at the base, curved over slightly at the top, glabrous with a few glandular hairs at the apex; anthers c.1 mm long, thecae divaricate and very narrow, glabrous, drying much darker than the filaments, with a distinctive pointed tip appearing like a hook or beak, not coherent; staminodes 3, c.5 mm long. *Gynoecium* c.30 mm overall; disc cupular with undulating margin, c.2 mm long, glabrous; ovary glabrous at the base becoming densely hairy after c.4 mm with the margin of indumentum somewhat lobed; style densely hairy; stigma bilobed, lobes vertical or spreading, c.3 × 2 mm, with short glandular hairs. *Fruits* ovoid (immature), c.15 × 11 mm, glabrous at the base, becoming densely hairy at apex; style and calyx not persistent.

Distribution. Central Sulawesi: Luwuk (see Fig. 11).

Habitat and ecology. Lower montane forest at c.980 m.

Etymology. Named after its distinctive red bracts.

Proposed IUCN conservation category. A lack of specimens of *Cyrtandra rubribracteata* precludes estimations of EOO and AOO. It is known with certainty from only one location, Mount Hek in Central Sulawesi, because it has not been possible to accurately georeference the earlier collection by Eyma (*Eyma* 3909). As with the other species described from this locality (e.g. *Cyrtandra albiflora*), this species does not receive any formal protection (UNEP-WCMC & IUCN, 2016). We suggest the



Fi g. 15. *Cyrtandra rubribracteata* Karton. & H.J.Atkins, sp. nov. A, Habit; B, anthers; C, gynoecium; D, corolla, longitudinal section; E, calyx, longitudinal section; F, fruit; G, bracteole; H, flower, lateral view; I, inflorescence. Drawn from *Hendrian* et al. 968 (E).

category Vulnerable (VU) for this species, using the criterion VUD2, because it is a population with a very restricted AOO or number of locations and, as such, is prone to the effects of human activities or stochastic events and is thus capable of becoming Critically Endangered or even Extinct in a short period of time, but emphasise the importance of carrying out further survey work in this region.

Additional specimen examined. **Central Sulawesi**: Luwuk Regency, between Camp I and Camp II, 28 ix 1938, *Eyma* 3909 (BO, K, L).

This species is very distinctive owing to its narrowly oblong leaves with serrate margins, large, dull red inflorescence bracts and unusual, somewhat beaked, anthers. No other species from Sulawesi recorded so far has these distinctive anther appendages. There are, however, a number of species from Borneo recorded with a 'conspicuous apiculus' on the anthers, such as *Cyrtandra prostrata* Kraenzl. and *Cyrtandra paxiana* Lauterb.

Acknowledgements

We thank the curators of the herbaria cited in the text for loans of material; Claire Banks for the detailed illustrations; Steve Scott, Sadie Barber and Nathan Kelso for great care of the living collections at RBGE; Wisnu Ardi, Sadie Barber, Axel Poulsen and Daniel Thomas for permission to use their photographs; and the RBGE Sibbald Trust for funding a visit to RBGE for one of the authors (AK) to consult the collections and collaborate on the paper.

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Received 24 October 2017; accepted for publication 9 February 2018; first published online 27 March 2018